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A REVISION OF THE GENUS *HIPPOSIDEROS*

J. E. HILL

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A REVISION OF THE GENUS *HIPPOSIDEROS*

BRITISH MUSEUM
31 OCT 1963
NATURAL HISTORY

BY

J. E. HILL
Department of Zoology
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A REVISION OF THE GENUS *HIPPOSIDEROS*

By J. E. HILL

SYNOPSIS

A taxonomic revision of the Microchiropteran genus *Hipposideros* is presented in this study which is primarily devoted to an examination of the genus at the specific and higher levels, with marked emphasis on the detailed diagnosis of its numerous species, their relationships, supraspecific groupings and probable phylogeny.

INTRODUCTION

THIS revision is based on the unequalled collections of the British Museum (Natural History), which contain an extensive series of the genus *Hipposideros*, complemented by a wealth of type specimens, and is principally concerned with the classification of the genus at the specific and higher levels. Detailed monographic treatment at the subspecific level would entail larger series than are at present available for many subspecies and to avoid uneven treatment of the genus has not been undertaken, although wherever possible some note has been taken of subspecific variation. Attention has been directed explicitly to the determination of the relationships between the species and species groups of this large genus and for this purpose detailed study has been concentrated at the level of the species. The results of this study are presented in the form of diagnoses of the numerous species included within *Hipposideros*, often based on the original material, in many cases supported by a further series of specimens, and of the species groups into which the genus can be divided. It has been possible to determine relationships between species, especially among those hitherto inadequately described or poorly known and to determine the validity and extent of the supraspecific groupings within the genus. The subsequent study of these groupings and their relationships has suggested a classification of *Hipposideros* and has given some indication of phylogeny within the genus. All measurements are in millimetres : forearm lengths are given in the form of histograms in the text, while minima, maxima and means (in parentheses) of representative cranial dimensions appear in a terminal table.

Genus ***HIPPOSIDEROS*** Gray, 1831

Hipposideros Gray, 1831 : 37. Type species by subsequent designation (Sclater (1901 : 116)) *Vespertilio speoris* Schneider.

Hipposiderus Gray, 1834 : 53. Emendation.

Phyllorrhina Bonaparte, 1837 : fascicule 21 (sub. *Rhinolophus ferrum-equinum*). Type species by subsequent designation (Sclater (1901 : 116)) *Rhinolophus diadema* Geoffroy.

Macronycteris Gray, 1866a : 82. Type species by monotypy *Rhinolophus gigas* Wagner.

Gloionycteris Gray, 1866a : 82. Type species by monotypy *Rhinolophus armiger* Hodgson.

Rhinophylla Gray, 1866a : 82. Type species by monotypy *Phyllorrhina labuanensis* Tomes.

Preoccupied by *Rhinophylla* Peters (1865a : 355, 1865b : 520), a genus of Phyllostomatidae.

Speorifera Gray, 1866a : 82. Type species by monotypy *Hipposideros vulgaris* Blyth = *Rhinolophus larvatus* Horsfield.

Chrysonycteris Gray, 1866a : 82. Type species by monotypy *Hipposideros fulvus* Gray.

Doryrhina Peters, 1871a : 324. Type species by monotypy *Phyllorrhina cyclops* Temminck.

Sideroderma Peters, 1871a : 324. Type species by monotypy *Phyllorrhina fuliginosa* Temminck.

Ptychorhina Peters, 1871a : 325. Type species by monotypy *Rhinolophus caffer* Sundevall.

Cyclorhina Peters, 1871a : 326. Type species by subsequent designation (Tate (1941 : 354)) *Phyllorhina obscura* Peters.

Thyreorhina Peters, 1871a : 327. Type species by monotypy *Phyllorhina coronata* Peters.

Syndesmotis Peters, 1871a : 329. Type species by monotypy *Phyllorrhina megalotis* Heuglin.

Hipposiderus Blanford, 1888 : 637. Emendation.

Taxonomic history of the genus

The early generic history of *Hipposideros* is confused and the availability of the names employed for the genus has been discussed by Blanford (1888 : 637), Palmer (1904 : 327, 535) and Oey & Feen (1958 : 226). The first generic name to be applied exclusively to a horseshoe bat was *Rhinolophus* Lacépède, 1799, and this name, for type species *Vespertilio ferrum-equinum* Schreber, 1774, the European greater horseshoe bat, was gradually brought into general use for all species of horseshoe bat as each was discovered and made known to science. Later, Leach (1816 : 5) introduced *Phyllorhina* for type species (by monotypy) *Vespertilio minutus* Montagu, 1808, the lesser horseshoe bat of Great Britain and Ireland, listing a specimen presented to the British Museum by G. Montagu with the citation :

> *Phyllorhina minuta*
>
> Small Leafnose
>
> Torquay, Devon. G. Montagu, Esq.

This citation follows that for *Rhinolophus ferrum-equinum*. The combination *Phyllorhina minuta* employed by Leach is listed by Miller (1912 : 149) and Ellerman & Morrison-Scott (1951 : 115) as a nomen nudum and as a possible synonym of *Rhinolophus hipposideros hipposideros* (Bechstein), 1800. However, Leach has clearly applied a new generic name to the species described by Montagu, now called *Rhinolophus hipposideros minutus*. Oey & Feen (1958 : 226) state that Leach employed *Phyllorhina* as a subgeneric name within *Rhinolophus* for the lesser horseshoe bat from England, retaining the greater horseshoe bat within the nominate subgenus. Leach, however, used both names in the generic sense, calling the greater horseshoe bat *Rhinolophus ferrum-equinum* and the lesser horseshoe bat *Phyllorhina minuta*. As Oey & Feen point out, no subsequent author has arranged *Rhinolophus ferrum-equinum* and *Rhinolophus hipposideros* (of which *Vespertilio minutus* Montagu, 1808 is now considered to be the British subspecies) under different genera or subgenera. *Phyllorhina* Leach, 1816, must therefore be considered a junior synonym of *Rhinolophus* Lacépède, 1799.

Gray (1831 : 37) first recognized the characteristic distinctions of the hipposiderine noseleaf, and with a valid diagnosis proposed the generic name *Hipposideros* for a number of Asiatic species hitherto referred to *Rhinolophus*. Sclater (1901 : 116) designated *Vespertilio speoris* Schneider as its type species. In a later work, Gray (1834 : 53) referred to this genus, using the amended spelling *Hipposiderus*. Peters (1871a : 312) and Dobson (1876 : 58, 1878 : 127) have quoted this name and reference in their synonymies of the genus and were apparently unaware of the earlier citation as *Hipposideros*. Later, Gray (1838 : 492) reverted to the original spelling and provided a further brief diagnosis. *Hipposideros* Gray, 1831, however, did not gain general acceptance and a number of authors, including Peters (1871a : 312) and Dobson (1876 : 58, 1878 : 127) employed *Phyllorrhina* Bonaparte, 1831, often rendering the name as *Phyllorhina*. This name is generally cited from C. L. Bonaparte, 1831, Saggio di una distribuzione metodica degli Animali Vertebrati. Two versions of this work exist in the Library of the British Museum (Natural History). It was published in two sections, the first concerned principally with the homoiothermic animals and the second the poikilothermic animals. The second section includes a further part giving additions and corrections to the first section. The first publication of this work is apparently in an Italian journal, Giornale Arcadico di Scienze, Lettere ed Arti, published quarterly in Rome. The first section appears in the issue for January, February and March, 1831, tome 49, part 1, pp. 3–77, the part number referring only to the number of issue for any one year and appearing only on the binding. The second section appears in the issue for October, November and December, 1831, tome 52, part 4, pp. 129–209. In this version of the work the name (spelt *Phyllorrhina*) appears on p. 15 as follows, 40 referring to its position in the table of genera and 16 to the number of species the genus includes :

40. *Rhinolophus*, Geoffr.	Eur. As. Af. Oc.	16.
1. *Rhinolophus*, Leach		
2. *Phyllorrhina*, Leach		

The second version of this work in the Library of the British Museum (Natural History) consists of two separately bound sections, corresponding to the two sections of the work as published in the Giornale Arcadico. The first section is almost identical with that in the Giornale Arcadico, but has a title page, the heading Scienze omitted and has been separately paginated. It is dated 1831 and was printed by Antonio Boulzaler, the printer of the Giornale Arcadico. The entry quoted above appears on p. 16 of this version of the work, and this apparently is the version quoted by Peters (1871a : 312), Dobson (1876 : 58, 1878 : 127), Blanford (1888 : 637), Palmer (1904 : 535), Sherborn (1929 : 4932) and Oey & Feen (1958 : 226) who without exception cite the name as *Phyllorhina*. The second section of the work has been similarly treated in the second version, with the addition of a title page, the omission of the heading Scienze and with separate pagination, but is dated 1832, suggesting that this separately bound version, quoted by authors, is but a reprint of the version printed in the Giornale Arcadico. It is not clear from the citation whether Bonaparte in this work employed *Phyllorrhina* as a subgenus of *Rhinolophus* in the sense of its generic usage by Leach (1816 : 5) or in the sense of *Hipposideros* as proposed by Gray (1831 : 37). In any case, the absence of diagnosis or of type species invalidates its proposal as a new name, as recognized by Palmer (1904 : 535), Sherborn (1929 : 4932) and Oey & Feen (1958 : 226).

Bonaparte (1837 : fascicule 21) under *Rhinolophus ferrum-equinum*, revived *Phyllorrhina* as a subgeneric name for the first section of *Rhinolophus* as listed by Temminck (1835 : 1–24), corresponding to the genus *Phyllorhina* of subsequent authors. Bonaparte gives a brief diagnosis and Sclater (1901 : 116) has designated *Rhinolophus diadema* Geoffroy as its type species. It was subsequently raised to generic rank by Peters (1852 : 31) who cited it, however, from Bonaparte (1831). Blanford (1888 : 637) rejected *Phyllorrhina* Bonaparte, 1837 on the grounds that *Hipposideros* Gray, 1831 had priority and that the name, which he rendered as *Phyllorhina*, had been originally proposed by Leach for a species of *Rhinolophus* and could not therefore be used for another genus. Palmer (1904 : 535) and Sherborn (1929 : 4932) reject it on ground of homonymy with *Phyllorhina* Leach, 1816, although both correctly citing the name as *Phyllorrhina*. Oey & Feen (1958 : 226) reject the name since at that time the alteration in spelling was considered insufficient under the International Code of Zoological Nomenclature to revive an unavailable generic name. However, Article 56(a) of the International Code of Zoological Nomenclature, 1961 states explicitly that two genus-group names are not to be considered homonyms even if the difference between them is due only to one letter, although it is recommended (Appendix D.3) that the proposal of such names should be avoided. Under these circumstances, therefore, *Phyllorrhina* Bonaparte, 1837, cannot be held to be a homonym of *Phyllorhina* Leach, 1816, and must be regarded as available within *Hipposideros* if subgeneric division of that genus is required.

Earlier students of the genus or of parts of it include Temminck (1835), Gray (1838, 1866a), Peters (1871a), Dobson (1876, 1878), Andersen (1905, 1906a, 1906b, 1918), Tate (1941) and Aellen (1952, 1956a, 1956b). Gray (1831) originally associated seven Asiatic species with the genus *Hipposideros*. Temminck (1835) reviewed the genus *Rhinolophus* in some detail, but made no formal recognition of the separation of that genus introduced by Gray. This author instead separated *Rhinolophus* into two sections, the first of these corresponding to *Hipposideros* of Gray (1831) or to *Phyllorhina* of later authors such as Peters (1871a) and Dobson (1876, 1878), adding a number of species to those attributed to *Hipposideros* by Gray and including an African species for the first time. Gray (1838) gave a brief review of *Hipposideros* and added a number of Asiatic species to the genus as listed by Temminck. Later, Gray (1866a) proposed six new generic names for species hitherto referred to *Hipposideros*. Peters (1871a) reduced these to subgenera and proposed six further subgeneric names. This work, the first critical study of the genus, thus greatly divided it but at the same time grouped under numerous subgeneric names the many species and their synonyms that had accumulated since Temminck and Gray first studied the genus as a whole. Gray (1866a) and Peters (1871a) were principally concerned with the diagnosis of the species groups into which *Hipposideros* is divisible, and although no great use has been made by other authors of subgenera within the genus, their subgenera in a number of cases have been recognized as species groups by most subsequent authors. Dobson (1876, 1878) placed the names proposed by Gray in the synonymy of *Phyllorhina* (=*Hipposideros*) and did not mention the subgeneric groupings of Peters, but at the specific level greatly amplified the revisionary work begun by Peters and provided detailed descriptions of the ears and noseleaves of individual species.

Andersen (1905, 1906a, 1906b) began the first modern detailed revisionary work on the genus with studies of the *diadema*, *armiger*, *commersoni* and *caffer* groups, and in Andersen (1918) Oldfield Thomas published on his behalf a compilation of diagnostic characters presented in the form of keys to the species and subspecies of some of the groups of *Hipposideros*, including brief diagnoses of a number of new forms. This work was probably an extract from a detailed revision upon which Andersen was working at the time of his disappearance and which was never completed. Tate (1941) in a comprehensive review of much of the genus greatly amplified the work of Gray, Peters and Andersen in the definition and diagnosis of its major groups, retaining for the most part the divisions originally proposed by Gray and Peters and allocating to them the species and subspecies more recently proposed. Tate, however, was primarily concerned with the Asiatic species of the genus and made no detailed survey of its African representatives, touching only briefly on their relationships to their Asiatic congeners. His work is nevertheless the only extensive survey of the genus since it was studied by Peters (1871a) and Dobson (1876, 1878) and has provided an excellent basis for its further revision. Although subsequent authors, notably Aellen (1952, 1956a, 1956b), have made valuable contributions to our knowledge of *Hipposideros*, especially to that of its African members, no student since Peters (1871a) and Dobson (1876, 1878) has attempted revisionary study of the genus as a whole, and it now stands badly in need of synthetic study.

Morphological criteria in the genus

The external features of the genus *Hipposideros* have been described by Dobson (1878 : 127) and the principal features of its skull by Miller (1907 : 111), while Tate (1941 : 357) has reviewed the major diagnostic criteria of importance within the genus. As might be expected of so large a genus, it displays a wide range of variation both externally and cranially. The ears, exceptionally united at the base by a low band of integument, vary in outline from comparatively short, broad and rounded or bluntly pointed to long, narrow and with an acute point. Their anterior or inner edge is generally convex, their posterior or outer edge straight or with a shallow concavity or emargination just behind the tip. Some species exhibit a well-defined internal fold at the antitragal lobe, in others absent or represented by a thickening of the membrane of the ear at this point. The external surface of the ear is usually naked except at its base but in some species can be covered with body fur for one half to two thirds the length of the ear. The nasal foliations are complex and consist basically of three sections, in this paper described as the anterior, intermediate and posterior noseleaves. The noseleaf in many species is flanked by one or more lateral supplementary leaflets, of which in some cases one may extend anteriorly beneath the anterior leaf on to the upper lip, sometimes forming a complete supplementary leaflet encircling the muzzle beneath the anterior leaf. The anterior noseleaf, extending over the upper lip, is the horseshoe of earlier authors, and is rarely much modified but occasionally displays a narrow median emargination. The nostrils open in paired depressions in the centre of this leaf, the narial openings separated by an internarial septum which is usually narrow or only slightly inflated but which may be bulbous, inflated or specialized to form a disc-like structure between the nostrils. Lateral narial lappets project from the outer walls of the narial depressions and together with the internarial septum may become modified to form deep pockets in which lie the narial apertures. The intermediate part of the noseleaf lies immediately behind the narial depressions, forming their posterior boundary, and is a cushion-like structure extending transversely across the entire noseleaf. It may be variously modified by the development of raised median and lateral eminences or ridges, or of a median club-like structure. Its posterior margin forms the base of the posterior leaf, an erect structure with a smooth or sometimes slightly lobulated upper edge, usually convex in outline but on occasion slightly triangular or specialized by the development of a median projection. The anterior face of the posterior leaf is more or less concave, the concavity smooth or divided by one or more vertical septa, enclosing small cells or pockets. The posterior face is usually smooth but in some species is modified by the development of a transverse supplementary structure with a serrated upper edge. The nasal foliations exhibit an exceptionally wide range of variation within the genus from small, comparatively simple structures showing little or no evidence of specialization to large, greatly modified structures completely covering the entire muzzle. A frontal sac, usually less developed in female specimens than in male, with its opening behind the posterior noseleaf, is to be found in a number of species, while a few species are noted for the development, especially in males, of transverse fleshy lobate prominences on each side of the opening of this sac.

The skull demonstrates a similarly wide range of variation, especially in the rostral, palatal and sphenoidal regions. Its basic outline varies from elongate and narrow, the zygomatic width less than or equal to the mastoid width, to short and comparatively broad with the zygomatic width exceeding the mastoid width of the skull. The braincase is generally elongate and never globose, and in some species is somewhat inflated. Sagittal and lambdoid crests are usually present and in the larger species are often greatly developed. The interorbital region is usually markedly constricted but exceptionally is broader with no sharp constriction between the braincase and the rostrum. The supraorbital ridges in some species are low and poorly defined and in others are well defined and prominent : they may partially enclose a frontal depression, itself sometimes absent. The rostrum, rounded in outline in some species, is in others more markedly pentagonal. It exhibits paired, inflated rostral eminences anterior to the anteorbital region, separated from each other by a shallow groove. The rostrum is expanded laterally to a greater or lesser degree, and in some species is markedly flattened and more greatly ossified. Considerable variation is displayed in the form of the premaxillae, which basically form a projecting structure with a V-shaped or U-shaped junction with the maxillae. Considered together, they vary from a narrow oblong structure not greatly expanded posteriorly at its junction with the maxillae to a wide structure almost filling the anterior palatal emargination with a wide, sometimes fan-shaped union with the maxillae. Their lateral edges may be deeply notched so that with the maxillae they form the walls of the anterior palatal foramina. In some species, delicate anterior enclosing processes are developed to form the anterior walls of these foramina : these processes in other species completely enclose the foramina which are thus contained within the premaxillae. The anterior palatal foramina in some species are small and rounded and in others are large and oval, elongate or slit-like. The palate is short and broad, the palation usually more or less U-shaped or square, with or without a median emargination or post-palatal spicule. The mesopterygoid fossa is wide and the pterygoids vary considerably in relative length between species. The sphenoidal bridge, flanked by rounded or elongate lateral apertures, usually partially conceals them but in some species is very markedly constricted. A sphenoidal depression is usually present. The cochleae typically are approximately equal in width to their distance apart but exceptionally may be greatly enlarged so that their width is equal to six or eight times this distance. The upper incisors are usually bilobed : the outer lobe, however, is present in varying degrees of obsolescence and in some species is virtually obsolete. The upper canines sometimes have low anterior or posterior cusps. The anterior upper premolar (pm^2) is small or minute, often extruded outwards from the toothrow so that the canine and the second upper premolar (pm^4) are in contact or nearly so : rarely the anterior upper premolar (pm^2) is absent. The posterior cusp of the third upper molar is usually obsolescent or obsolete and its third commissure undeveloped, with the W-pattern of the tooth incomplete : exceptionally the third cusp may be more or less unreduced and the commissure present with the W-pattern of the tooth virtually complete. The crown area of the outer lower incisors in some species is less than or equal to the crown area of the inner teeth : in other species it is greater than the crown area of the inner teeth. The anterior lower premolar (pm_2), sometimes almost equal in size to the second lower premolar (pm_4), is more usually reduced, sometimes to one quarter or one third the size of the second tooth.

Supraspecific groupings within the genus

Tate (1941 : 355) has rightly pointed out that the characters of the numerous species currently included within *Hipposideros* seldom combine to indicate clearly evident evolutionary trends. As this author says, such evidence in this genus is perplexing and often contradictory, and the morphological criteria in *Hipposideros* apparently represent tendencies latent in perhaps all of its species, active in some and quiescent in others. Similarly, such criteria combine but rarely to form an aggregate of features defining natural groups of species within the genus. Despite this, Peters (1871a) was able to discern twelve subgenera in *Hipposideros* (albeit with fewer species under consideration than are currently included in the genus) and Tate (1941) was able to reduce these only to eleven major species groups, while Aellen (1954) has added a further group to those defined by Tate. A review of the morphological features of these groups indicates that considerable similarity exists between several of them, and that some at least may be separated only with difficulty from each other. It is clearly evident that the great degree of subdivision advocated by Peters is wholly unjustified and that subgeneric division at this level is unwarranted.

It is possible to discern three primary divisions in *Hipposideros*. One, in general a more primitive section, appears to represent the basic group of the genus from which the other, more specialized sections have been derived. It has itself developed a number of specialized forms as well as retaining species exhibiting comparatively simple and unspecialized features. Members of the groups allocated to this section of the genus are generally of small size, with broad, usually rounded ears, often modified by the presence of an internal fold or thickening at the antitragal lobe, while in most the noseleaves are comparatively simple. Lateral supplementary leaflets may be absent : one leaflet may be incipient or present and in some two lateral leaflets are to be found. The skull is more or less elongate and narrow, with an inflated braincase, the zygomatic width less than or not greatly exceeding the mastoid width. The upper incisors are usually weak and lack much of their outer lobe, while the crown dimensions of the outer lower incisors only exceptionally greatly exceed those of the inner lower incisors. The *megalotis*, *bicolor*, *calcaratus* and *galeritus* groups of Tate (1941) and the *curtus* group of Aellen (1954) fall into this division. Of these, the *megalotis* group, containing only the African species *megalotis*, is perhaps the most primitive. Despite the uniquely conjoined ears of *H. megalotis* and its large outer incisors, which in crown area greatly exceed the inner incisors, such characters as its small, simple noseleaf lacking lateral leaflets, and its elongate skull with inflated braincase and weak upper incisors suggest that it is not far removed from the basal stem of *Hipposideros*. The *bicolor* and *calcaratus* groups of Tate (1941) are for the most part little more specialized, their species usually with simple noseleaves which either lack lateral leaflets or have one leaflet only, sometimes in incipiency. They have an elongate, narrow skull similar in outline to that of *H. megalotis*. The *galeritus* group of Tate (1941) represents a more specialized derivative of *bicolor*, its species with two lateral leaflets and a more specialized, shorter, wider skull. The *bicolor* and *galeritus* groups as understood by Tate (1941) include a number of isolated species, usually monotypic and in some cases displaying complex developments of the noseleaves. These, although in some instances representing independent but relatively minor lines of modification, in others are highly specialized offshoots of the *bicolor* and *galeritus* types, or of the stem connecting them. In many respects such species connect the two groups, while the *calcaratus* group appears to be a derivative of the *bicolor* type. In the present work, the *bicolor*, *calcaratus* and *galeritus* groups as they are defined by Tate (1941), together with the *curtus* group of Aellen (1954), are united to form a single group, for which the earliest name is *bicolor*.

The second primary division of the genus contains only the highly specialized *cyclops* and *muscinus* groups of Tate (1941), here united to form a group for which *cyclops* is the prior name, restricted to Papua, northern Australia and West Africa. This group exhibits modifications of the noseleaves so peculiar that despite the curious distributional pattern of its members they must be considered to share a common if remote origin. It shares some features with the *bicolor* group, notably the small size of some of its members, but the species allocated to the *cyclops* group have longer, narrower ears, sharply triangular, with little or no antitragal modification. Their noseleaves have two lateral leaflets and are uniquely distinguished in the genus by the second lateral leaflet, which forms an integral part of the posterior leaf and in Australasian species extends anteriorly beneath the anterior leaf, over the upper lip. The noseleaves are further specialized by the development of median tubercles or club-like processes from the intermediate and posterior noseleaves. The skull is less elongate and comparatively wider than in the *megalotis* and *bicolor* groups : the upper incisors are weak and the outer lower incisors are very slightly larger in crown area than the inner lower incisors. The least specialized members of the group share some degree of affinity with the *bicolor* group and it seems likely that the origins of the *cyclops* group lie remotely with the *bicolor* group of species.

A third division of *Hipposideros* is represented by the *pratti*, *armiger*, *speoris*, *diadema* and *commersoni* groups of Tate (1941). Their members are characterized principally by their larger size, their smaller, triangular ears, which usually lack any antitragal modification, by their comparatively simple noseleaves, which have two or more commonly three or four lateral leaflets, and by their comparatively shorter, broader skulls, which have wider, more expanded zygomata. In the species allocated to these groups the upper incisors are stout and retain much of the outer lobe, while the crown area of the outer lower incisors is greater than that of the inner lower incisors, sometimes greatly so. Monotypic species are rare among these groups, and there are no species with the exotic modifications such as are to be found in the first and second divisions. There are, however, some indications of specialization in the presence of greatly developed transverse supplementary lappets behind the posterior leaf in the *pratti* group and in the slightly trilobate posterior leaf of the *armiger* group. The *commersoni* group of Tate (1941) appears to be the African representative of the Austro-Malayan *diadema* group as understood by that author, and in the present work these have been united to form a single group for which the prior name is *diadema*.

The primary divisions of the genus indicate three general but distinct evolutionary trends within *Hipposideros*. One, exemplified by the *megalotis* and *bicolor* groups, is towards small or medium size and development and proliferation of the noseleaves, combined with a corresponding increase in the size of the ears and only exceptionally with extensive cranial modification, the skull generally elongate and not greatly widened. The aberrant *cyclops* group represents a second trend sufficiently differentiated as to justify its separation from that shown by *megalotis* and *bicolor*, with greatly developed noseleaves and much modification of the ears and auditory region of the skull. This group displays a number of unique features, especially in the combination of small size, large ears and complex noseleaves with a broadened skull in its Australasian species and in the combination of large size, large ears and complex noseleaf with a very wide skull in its West African species. A third trend, exemplified by the *pratti*, *armiger*, *speoris* and *diadema* groups, is towards greater size, without extensive increase in the size and complexity of the ears and noseleaf, but with corresponding broadening of the skull. Each of these divisions include subsidiary lines of development, and while this view is perhaps an over-simplification of major evolutionary trends in *Hipposideros* it is clear that the genus cannot be divided readily into more primitive and more advanced groups of species. It can only be stated in general terms that these divisions represent three more or less parallel lines of development within the genus. However, the *megalotis-bicolor* section includes a number of species which are not greatly specialized, and is therefore to be regarded as the more primitive. It has at the same time developed species which in many of their features are as highly developed as those included in the *cyclops* section or in the section containing the *pratti*, *armiger*, *speoris* and *diadema* groups. The three primary groups express to some extent at least the major lines of development that have occurred within *Hipposideros* : the divisions between them, however, are not clearly defined and there is manifestly no justification for the extreme subdivision of the genus practised by Peters (1871a) in his recognition of twelve subgenera of *Hipposideros*. The genus appears instead to consist of an aggregation of loosely defined groups of species, each exhibiting varying combinations of characters, some highly specialized. Tate (1941) recognized this and divided the genus into eleven species groups but did not study its African species in detail. In the present work these have been related to Asiatic species groups and through the combination of some of the groups of Tate the varying levels of development within *Hipposideros* have been expressed by the division of the genus into seven species groups, one divided into two subgroups. The groups are listed in the following summary, with their included species, excluding *doriae* Peters, probably identical with *sabanus* and which therefore has been excluded from the following discussion.

megalotis group
- *megalotis* Heuglin

bicolor group
- *bicolor* subgroup
  - *bicolor* Temminck
  - *ater* Templeton
  - *fulvus* Gray
  - *cineraceus* Blyth
  - *nequam* Andersen
  - *calcaratus* Dobson
  - *cupidus* Andersen
  - *coronatus* Peters
  - *ridleyi* Robinson & Kloss
  - *jonesi* Hayman
  - *dyacorum* Thomas
- *galeritus* subgroup
  - *pygmaeus* Waterhouse
  - *galeritus* Cantor
  - *breviceps* Tate
  - *curtus* Allen
  - *fuliginosus* Temminck
  - *caffer* Sundevall
  - *beatus* Andersen
  - *coxi* Shelford
  - *papua* Thomas & Doria

- *bicolor* group
  - *bicolor* subgroup (*contd.*)
    - *sabanus* Thomas
    - *obscurus* Peters
    - *marisae* Aellen
- *cyclops* group
    - *cyclops* Temminck
    - *camerunensis* Eisentraut
    - *muscinus* Thomas & Doria
    - *wollastoni* Thomas
    - *semoni* Matschie
    - *stenotis* Thomas
- *pratti* group
    - *pratti* Thomas
    - *lylei* Thomas
- *armiger* group
    - *armiger* Hodgson
    - *turpis* Bangs
- *speoris* group
    - *abae* Allen
    - *larvatus* Horsfield
    - *speoris* Schneider
- *diadema* group
    - *lankadiva* Kelaart
    - *schistaceus* Andersen
    - *diadema* Geoffroy
    - *dinops* Andersen
    - *inexpectatus* Laurie & Hill
    - *commersoni* Geoffroy

Forty-three species are recognized, of which it has been possible to examine all but *coronatus* and *marisae*. The *bicolor* group as here understood includes the *bicolor*, *galeritus* and *calcaratus* groups of Tate (1941) and is a complex of related species not readily separable into different groups. The *cyclops* group listed by Tate (1941) has been incorporated into the *muscinus* group as recognized by that author to form a *cyclops* group, while the *commersoni* group of Tate (1941) is closely related to the *diadema* group and has been united with it. Relationships between the groups are briefly summarized in the form of a diagram (Fig. 1).

The genus is remarkable for its high content of monotypic species, with no fewer than twenty-seven of its forty-three species not divided into subspecies. Of the remainder, seven are divided into two subspecies and one into three, while only eight species have more than three subspecies. The distribution of subspecies in the species groups of *Hipposideros* is shown in Table 1. The *megalotis*, *bicolor* and *cyclops* groups contain by far the majority of monotypic species and while some of

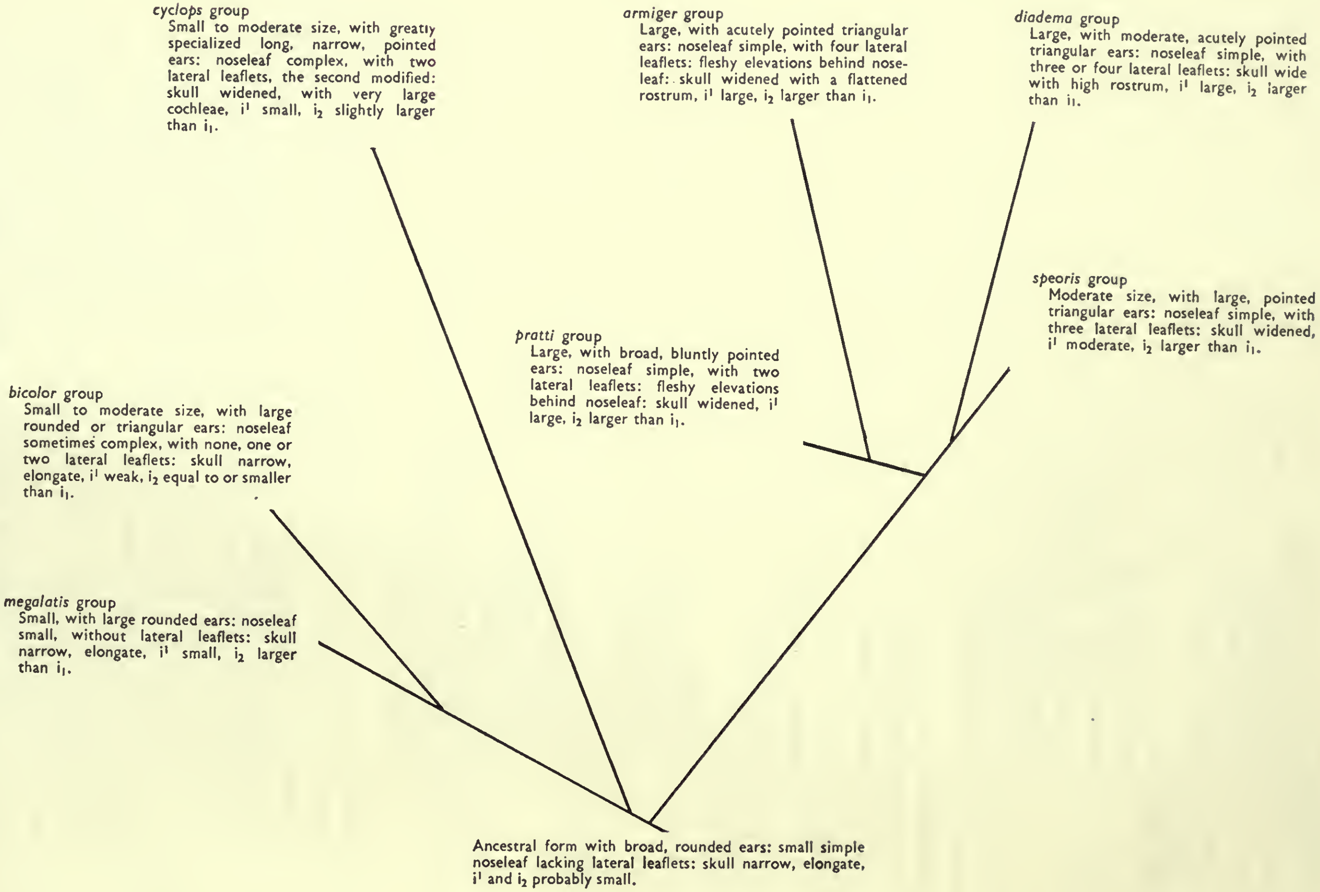

cyclops group
Small to moderate size, with greatly specialized long, narrow, pointed ears: noseleaf complex, with two lateral leaflets, the second modified: skull widened, with very large cochleae, i^1 small, i_2 slightly larger than i_1.
armiger group
Large, with acutely pointed triangular ears: noseleaf simple, with four lateral leaflets: fleshy elevations behind noseleaf: skull widened with a flattened rostrum, i^1 large, i_2 larger than i_1.
diadema group
Large, with moderate, acutely pointed triangular ears: noseleaf simple, with three or four lateral leaflets: skull wide with high rostrum, i^1 large, i_2 larger than i_1.
speoris group
Moderate size, with large, pointed triangular ears: noseleaf simple, with three lateral leaflets: skull widened, i^1 moderate, i_2 larger than i_1.
pratti group
Large, with broad, bluntly pointed ears: noseleaf simple, with two lateral leaflets: fleshy elevations behind noseleaf: skull widened, i^1 large, i_2 larger than i_1.
bicolor group
Small to moderate size, with large rounded or triangular ears: noseleaf sometimes complex, with none, one or two lateral leaflets: skull narrow, elongate, i^1 weak, i_2 equal to or smaller than i_1.
megalatis group
Small, with large rounded ears: noseleaf small, without lateral leaflets: skull narrow, elongate, i^1 small, i_2 larger than i_1.
Ancestral form with broad, rounded ears: small simple noseleaf lacking lateral leaflets: skull narrow, elongate, i^1 and i_2 probably small.

FIG. 1. Group relationships in *Hipposideros*

these are clearly closely related, others are separated from each other by very distinctive external and cranial features. Rather than representing comparatively recent developments within the genus, from the wide divergence of their isolating characters and their usually restricted distribution, these species appear to be relicts of a rather remote phase of radiation within *Hipposideros*. The three species groups themselves support this contention, their considerable dissimilarities suggesting their separation at an early stage in the evolution of the genus. The *megalotis* group is monotypic and of very restricted distribution, while the *bicolor* group contains a wide diversity of loosely allied species, few of them successful and widespread, and many apparently representing independent lines of development. These groups are widely separated from the *cyclops* group, also of restricted distribution and so distinctively specialized as to demand a long period of modification. The *bicolor* and *cyclops* groups have both Asiatic and African representatives, whose wide separation from each other in a number of basic features indicates that the partition of each parent group into Asiatic and African sections now no longer continuous was evidently a remote event. African representatives of the *bicolor* group are rather less distantly removed from their Asiatic congeners than are the African *cyclops* and *camerunensis* from the Australasian *muscinus* and its allies and the *bicolor* group includes a few species demonstrating to a limited extent the connection between its Asiatic and African species. However, the evidence of this connection is tenuous and the development of the group in the Asiatic and African regions apparently represents two independent, parallel lines of modification from a common but remote origin, often displaying considerable similarity and convergence, and with a number of independent offshoots in each region.

Group	Number of species	Number of monotypic species	Number of species divided into two subspecies	Number of species divided into three subspecies	Number of species divided into more than three subspecies
megalotis group	1	1	–	–	–
bicolor ,,	23	16	3	–	4
cyclops ,,	6	6	–	–	–
pratti ,,	2	2	–	–	–
armiger ,,	2	–	1	1	–
speoris ,,	3	1	1	–	1
diadema ,,	6	1	2	–	3
Totals	43	27	7	1	8

TABLE 1. Distribution of species and subspecies among the species groups of *Hipposideros*.

The *pratti*, *armiger*, *speoris* and *diadema* groups contain fewer isolated, monotypic species and represent two allied lines of modification developed independently but more or less parallel to the development of the *megalotis*, *bicolor* and *cyclops* groups. One, exemplified by the wholly Asiatic *pratti* and *armiger* groups, is towards specialization of the noseleaves and rostral region. The *pratti* group, with two species, both monotypic, is of very restricted distribution and is evidently related rather distantly to the more widespread *armiger* group. The other trend includes the *speoris* and *diadema* groups, and is towards great size and its corresponding modifications of the skull, both groups having representatives in the Asiatic and African regions. In the *speoris* group, less specialized than *diadema*, the sole African species is less closely related to its Asiatic congeners than the African representative of the *diadema* group is to the Asiatic species of the group, and the *speoris* and *diadema* groups apparently represent a rather more recent phase of radiation than do the *pratti* and *armiger* groups. These four groups differ widely from the *megalotis*, *bicolor* and *cyclops* groups, and it is evident that their separation occurred at a very early stage in the evolution of the genus.

The seven species groups into which the genus is divided in the present paper may be keyed :

1 Ears united at the base by a low frontal band . . . *megalotis* group (p. 17)
Ears not united 2
2 Ears long and narrow, pointed (Figs. 20, 22–25) : cochleae greatly expanded, their width equal to at least four times their distance apart . *cyclops* group (p. 72)
Ears short, broad, rounded or triangular : cochleae not expanded, their width approximately equal to their distance apart 3
3 Ears rounded or broadly triangular, bluntly pointed : upper incisors weak, the outer lobe obsolescent or obsolete ; crown area of outer lower incisors equal to or only slightly greater than that of the inner lower incisors . . *bicolor* group (p. 18)
Ears triangular, pointed : upper incisors strong, usually retaining much of the outer lobe ; crown area of the outer lower incisors much greater than that of the inner lower incisors 4
4 Noseleaf with two lateral supplementary leaflets : frontal depression well-defined ; maxillae elongated . . . . *pratti* group (p. 87)
Noseleaf with three or four lateral supplementary leaflets : frontal depression lacking or shallow ; maxillae not elongated 5
5 Noseleaf with upper edge of posterior leaf slightly lobate, the posterior leaf narrower than the anterior leaf : rostral eminences not inflated and rostrum flattened ; a distinct discontinuity between roofs of narial and mesopterygoid canals *armiger* group (p. 91)
Noseleaf with upper edge of posterior leaf forming an arc of a circle, the posterior leaf equal in width to the anterior leaf : rostral eminences moderately inflated and rostrum elevated ; roofs of narial and mesopterygoid canals not sharply discontinuous 6
6 Ears with a small projection at the antitragal fold : sphenoidal bridge narrow, not concealing lateral apertures ; pterygoid wings undeveloped *speoris* group (p. 94)
Ears without antitragal modification : sphenoidal bridge wide, partially concealing lateral apertures ; pterygoid wings expanded . . . *diadema* group (p. 103)

HIPPOSIDEROS MEGALOTIS group

This group contains only the isolated African species *Hipposideros megalotis* (Heuglin), which may be distinguished at once from all other species of the genus by the low band of integument uniting the ears at their base. Peters (1871a : 329) proposed subgeneric recognition for *megalotis* under the name *Syndesmotis*, largely on account of its conjoined ears, but Dobson (1878 : 151) ignored this separation and concluded from an examination of the type specimen that the species belonged to that section of *Hipposideros* typified by *H. bicolor* and its associated species. Senna (1905 : 275) provided a detailed account of two topotypical specimens of *megalotis* and raised *Syndesmotis* of Peters to generic rank. His diagnosis of *Syndesmotis* was the first comprehensive definition to appear and was based on the conjoined ears, notched, sinuous upper edge of the posterior noseleaf, low cranium, undeveloped sagittal crest, high occipital, elevated frontal, narrow basioccipital and the absence of the anterior upper premolars (pm$^{2-2}$) in *megalotis*, characters which he considered to render the species generically distinct from *Hipposideros*. However, apart from the first, these features are to be found in one or other of the remaining species groups of *Hipposideros*, and no later author has employed *Syndesmotis* in the subgeneric or generic sense. Tate (1941 : 357) first listed the species as *H.* (*Syndesmotis*) *megalotis* and postulated a relationship to the Megadermatidae but later (1941 : 359) listed *megalotis* as the sole species of the *megalotis* group. Hayman (1954 : 285) reviewed earlier accounts of the species, which hitherto had been known only from the type locality, Kérén, in Eritrea, and extended its range to the Kenya highlands. Later (1960 : 61) the same author recorded the species from Ethiopia.

There is little to justify the separation of *megalotis* from *Hipposideros*. Despite its uniquely specialized ears, and its expanded bullae, which are reminiscent of the *cyclops* group, *megalotis* is clearly a primitive species of the genus, allied in many respects to the less specialized species of the *bicolor* group. Such characters as its small, simple noseleaf lacking lateral leaflets, elongate skull with inflated braincase and narrow rostrum and its weak upper incisors display its affinities with *H. bicolor* and its allies. At the same time, an evidently long period of modification has led to the development of a greatly specialized auditory region, and to specialization of the dentition in the loss of the anterior upper premolars (pm$^{2-2}$) and considerable increase in the dimensions of the outer lower incisors, which greatly exceed the inner lower incisors in crown area. These features, together with its uniquely joined ears, adequately justify the position of *megalotis* as the sole member of an individual group of *Hipposideros*.

Hipposideros megalotis (Heuglin)

Phyllorrhina megalotis Heuglin, 1862 : 4, 8, Kérén, Eritrea.

The ears of *Hipposideros megalotis* are large, rounded, their posterior margins without a concavity behind the tip, and have a small internal fold at the antitragal lobe : they are haired for a little less than one half of their length. They are joined at the base by a low band of integument. The noseleaf is small and simple, and lacks lateral leaflets : the anterior leaf is unemarginated, the intermediate part of the leaf uninflated, with a low median eminence, while the posterior leaf is moderate, supported by three poorly defined ridges and with its upper edge slightly sinuous, more or less semicircular. The skull is small and elongate, with an inflated braincase and narrow rostrum. The sagittal crest is low and there are no supraorbital ridges. The frontal region is slightly elevated and lacks a frontal depression : the rostral eminences are moderately inflated. The zygomata are moderate, with a low jugal projection : the zygomatic width is less than the mastoid width. The anteorbital foramina are large and rounded, closed by a narrow bar of bone. The junction of the premaxillae with the maxillae is U-shaped and the incisive foramina are rounded and not enclosed within the premaxillae, their antero-posterior walls formed by the maxillae. The palation is U-shaped, with a median emargination, and the vomer projects slightly into the mesopterygoid fossa. The sphenoidal bridge is moderate and flanked by large, rounded lateral apertures. There is a shallow sphenoidal depression : the basioccipital is narrow and the cochleae large, their width equal to approximately three times their distance apart. The upper incisors are widely spaced and weakly bilobed, the outer lobe a little smaller than the inner lobe. The upper canines are slender, with a well-developed posterior cusp. The anterior upper premolar (pm^2) is absent and the posterior ridge of the third upper molar obsolescent. The outer lower incisors are much larger in crown area than the inner pair and the anterior lower premolar (pm_2) is one half the height and three quarters or more the length of the second lower premolar (pm_4).

APPROXIMATE DISTRIBUTION : Eritrea ; Ethiopia ; Kenya.

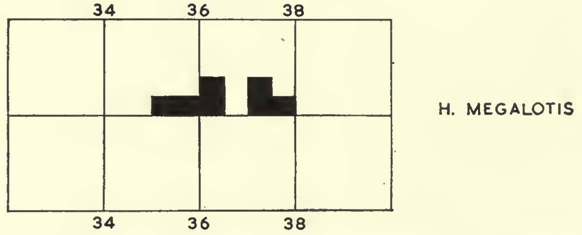


FIG. 2. Length of forearm in *Hipposideros megalotis*

HIPPOSIDEROS BICOLOR group

The *bicolor* group as here understood contains the *bicolor, calcaratus* and *galeritus* groups of Tate (1941) together with a number of species not studied or allocated to group by that author. The ears of members of the *bicolor* group are large, broad, rounded or more or less triangular in outline, bluntly pointed, with an internal fold or a thickening of the membrane of the ear at the antitragal lobe. Noseleaves within the group vary from the relatively unspecialized and simple structures of *bicolor* and its immediate allies to the complex, greatly developed, sometimes bizarre foliations of such species as *jonesi* or *coxi*. The number of lateral supplementary leaflets varies from none or incipiently one in the more primitive species of the group to one or more usually two in those more specialized, while *papua*, a somewhat anomalous species allocated to the *bicolor* group, has an incipient, very poorly developed third leaflet. Species allocated to this group have elongate, narrow skulls, with moderately inflated braincases and narrow rostra and an unspecialized auditory region, the cochleae never more than a little wider than their distance apart. Their upper incisors are weak, the outer lobe obsolescent or obsolete, while the crown dimensions of the outer lower incisors are less than or only slightly greater than those of the inner lower incisors. There is no good reason to divide the *bicolor* group into separate species groups : the *bicolor* and *calcaratus* groups of Tate (1941) clearly represent an aggregation of more primitive species while the *galeritus* group and its derivatives as understood by that author consists of more specialized species whose connection with *bicolor* and its immediate allies in some cases can still be traced. The group is of remote origin and is the most wide-ranging of the genus, distributed in one form or another from Africa to the New Hebrides and northern Australia, although it is almost equalled in this respect by the *diadema* group, which has a similar distributional pattern but extends eastward only to the Solomon Islands and does not enter Australia. It is by far the largest group within the genus and while it includes a number of unspecialized species, the group at the same time includes species which have developed this basic pattern into highly specialized elaborations.

The species allocated to the *bicolor* group may be divided into two loosely defined subgroups, corresponding approximately to the *bicolor* and *galeritus* groups of Tate (1941). The *bicolor* subgroup includes the *calcaratus* group of Tate (1941), which has few characters to distinguish it from *bicolor* and its allies, and is predominantly Indo-Australian in distribution, with two species extending its distribution to Africa. Its members are in general less specialized than those of the *galeritus* subgroup and usually have broader, more rounded ears, which in most cases have an internal fold at the antitragal lobe and are haired for one half or less of their length. Lateral supplementary leaflets as a rule are absent or are exceptionally represented by a single small leaflet. The skull is elongate and narrow, with an inflated braincase, the zygomatic width rarely exceeding the mastoid width. Although the subgroup includes some of the least specialized species of the genus, it contains also such more advanced derivatives as *dyacorum*, *sabanus* and *jonesi* exhibiting a considerable degree of specialization. The *galeritus* subgroup is represented in the Asiatic and Australasian regions by *galeritus* and its associated species and in the Ethiopian region by *caffer* and its allies. Its members are characterized by their usually more or less triangular ears, which often display a concavity in their posterior margins just behind the tip of the ear. The antitragal fold is less prominent and the ears are usually haired for about two thirds of their length. The noseleaves are in general more specialized and have two or exceptionally three lateral supplementary leaflets. Members of this subgroup have shorter, broader skulls than the members of the *bicolor* subgroup, with the zygomatic width exceeding the mastoid width. As in the *bicolor* subgroup, some species of the *galeritus* subgroup exhibit great elaboration of its basic pattern.

No definitive line of separation can be found between the subgroups, and they are linked by species exhibiting their respective characteristics in differing combinations. *Hipposideros sabanus* and *H. dyacorum* both lack lateral leaflets and have the comparatively simple noseleaf of the *bicolor* subgroup yet have the shortened, rather broadened skull characteristic of the *galeritus* subgroup. *Hipposideros obscurus* has likewise no lateral leaflets but has somewhat triangular ears and a short, broad skull. *Hipposideros marisae* has ears and noseleaf similar to those characteristic of the *galeritus* subgroup, but has one lateral supplementary leaflet and a somewhat elongate skull. *Hipposideros curtus* has two lateral leaflets and cranially resembles the *galeritus* type, but has the ears haired for only one half of their length. *Hipposideros fuliginosus* and *H. pygmaeus* have two lateral leaflets but have the sparsely haired ears and elongate skulls of the *bicolor* type, while *H. coxi* has two lateral leaflets and ears haired for two thirds of their length yet has an elongate, unbroadened skull. Such species serve to demonstrate the close affinity of the members of the *bicolor* group and its essential unity. This treatment of the group greatly extends the views of Tate (1941 : 358, 366) who recognized that the African *caffer* and its allies should be associated with his Asiatic *galeritus* group, but did not relate these species and their associates to those he included in the *bicolor* group as he defined it. The allocation of the African species of the *bicolor* group as here understood contrasts sharply with the views of Aellen (1952 : 62), who divided them widely by the recognition of a *caffer* group for *caffer* and its associated species *curtus*, *fuliginosus* and *beatus*, and later (1954 : 479, 480) recognized additionally a *jonesi* group for the sole species *jonesi* and a *curtus* group for the species *curtus* and *marisae*. *Hipposideros caffer* and its allies, together with *curtus*, are closely related to *galeritus*, and in the present work are referred to the *galeritus* subgroup, while *jonesi* and *marisae* have affinities with the *bicolor* subgroup, to which they are referred.

Possible relationships within the group are summarized in the form of a diagram (Fig. 3). Morphological characters in the group rarely combine to indicate definite trends, and the relationships of the numerous species comprising the *bicolor* group are not easily discerned and are difficult of definition. The considerable degree of elaboration of the noseleaves displayed by some species tends further to obscure their basic pattern. General tendencies discernible within the group are for the ears to become less rounded and more triangular, and for their posterior edges to develop a concavity just behind the tip. At the same time, an increase in the area of body fur extending over the outer surface of the ears can be seen, and the internal fold tends to become less prominent. Lateral supplementary leaflets are absent in the more primitive species of the group, more advanced species having one or more frequently two leaflets, while one species, *papua*, possesses a third leaflet, incipient and poorly developed. Cranially, the elongate, rather narrow outline of the skull in the primitive members of the group tends to become shorter and broader in those more advanced. These general trends, however, are obscured to a large extent by considerable overlap between a number of species, indicated in fig. 3 by enclosure between two parallel dotted lines. Such species exhibit varying combina-

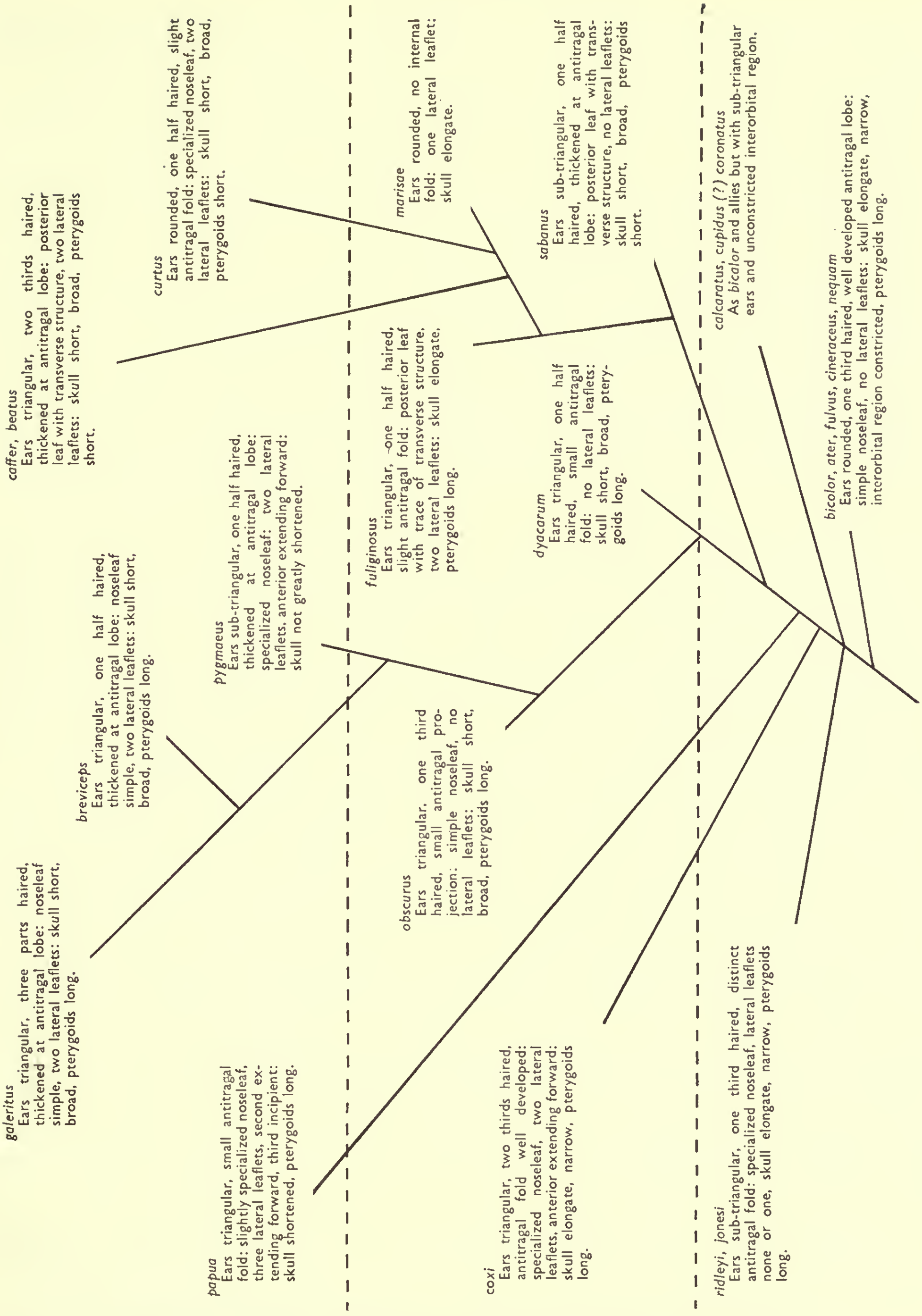

bicolor, ater, fulvus, cineraceus, nequam
Ears rounded, one third haired, well developed antitragal lobe: simple noseleaf, no lateral leaflets: skull elongate, narrow, interorbital region constricted, pterygoids long.
calcaratus, cupidus (?) coronatus
As bicolor and allies but with sub-triangular ears and unconstricted interorbital region.
ridleyi, jonesi
Ears sub-triangular, one third haired, distinct antitragal fold: specialized noseleaf, lateral leaflets none or one, skull elongate, narrow, pterygoids long.
sabanus
Ears sub-triangular, one half haired, thickened at antitragal lobe: posterior leaf with transverse structure, no lateral leaflets: skull short, broad, pterygoids short.
dyacarum
Ears triangular, one half haired, small antitragal fold: no lateral leaflets: skull short, broad, pterygoids long.
coxi
Ears triangular, two thirds haired, antitragal fold well developed: specialized noseleaf, two lateral leaflets, anterior extending forward: skull elongate, narrow, pterygoids long.
marisae
Ears rounded, no internal fold: one lateral leaflet: skull elongate.
fuliginosus
Ears triangular, one half haired, slight antitragal fold: posterior leaf with trace of transverse structure, two lateral leaflets: skull elongate, pterygoids long.
obscurus
Ears triangular, one third haired, small antitragal projection: simple noseleaf, no lateral leaflets: skull short, broad, pterygoids long.
curtus
Ears rounded, one half haired, slight antitragal fold: specialized noseleaf, two lateral leaflets: skull short, broad, pterygoids short.
pygmaeus
Ears sub-triangular, one half haired, thickened at antitragal lobe: specialized noseleaf: two lateral leaflets, anterior extending forward: skull not greatly shortened.
papua
Ears triangular, small antitragal fold: slightly specialized noseleaf, three lateral leaflets, second extending forward, third incipient: skull shortened, pterygoids long.
caffer, beatus
Ears triangular, two thirds haired, thickened at antitragal lobe: posterior leaf with transverse structure, two lateral leaflets: skull short, broad, pterygoids short.
breviceps
Ears triangular, one half haired, thickened at antitragal lobe: noseleaf simple, two lateral leaflets: skull short, broad, pterygoids long.
galeritus
Ears triangular, three parts haired, thickened at antitragal lobe: noseleaf simple, two lateral leaflets: skull short, broad, pterygoids long.

Fig. 3. Possible relationships in the *Hipposideros bicolor* group

tions of primitive and advanced morphological characters and must be regarded as transitional between the simplest members of the group and those most specialized, although some such as *coxi* display a high degree of individual specialization. A number of less general trends exist within the group and are confined in some cases to one or two species. Such a trend is found in *ridleyi* and *jonesi*, large species of the *bicolor* subgroup which have however developed the internarial septum to form a concave circular disc between and partially covering the nostrils : *jonesi* is more developed in this respect and additionally has a deeply pocketed posterior leaf reminiscent of that of *coxi*. Similarly, *calcaratus* and *cupidus* have developed a broad interorbital region and their zygomata are widened to an extent considerably exceeding the mastoid width, although in other respects both are very simple species with broad ears which possess an antitragal fold and with a simple noseleaf, lacking lateral leaflets. *Hipposideros coxi* has a highly complex noseleaf with two lateral leaflets, the anterior leaflet extending forwards beneath the anterior leaf to the median line and with the posterior leaf elaborated into a complex, deeply pocketed structure. Its skull, however, is comparatively elongate and narrow and basically is of the *bicolor* type. A trend towards *galeritus* is characterized by the retention of a skull architecturally rather like that of the *bicolor* type, although broadened, with long pterygoids and a short sphenoidal bridge. It can be traced through *dyacorum*, a simple species lacking lateral leaflets and with a comparatively elongate skull, *obscurus*, a species with a specialized noseleaf, no lateral leaflets and shortened skull and *pygmaeus*, similar to *obscurus*, but with a more specialized noseleaf and two lateral leaflets. The trend towards *caffer* is characterized by a shortening of the pterygoids and consequent extension of the sphenoidal bridge, and in some species by the development of a transverse, serrated structure from the rear face of the posterior leaf. It includes *sabanus*, a simple species lacking lateral leaflets but with a transverse supplementary structure behind the rear leaf and a short, broad skull with short pterygoids and *fuliginosus*, with two lateral leaflets, a trace of a supplementary structure behind the posterior leaf yet with an elongate skull with long pterygoids. This trend must include also *marisae*, with broad ears, one small leaflet and elongate skull, and *curtus*, with similar ears, two lateral leaflets and shorter, broadened skull with short pterygoids, two species further specialized by the considerable inflation of the internarial septum. *Hipposideros papua*, apparently derived from the stem leading to *galeritus* and *caffer*, is a highly specialized species unique in the *bicolor* group by the possession of three lateral supplementary leaflets, the third small and undeveloped. The anterior leaflet extends upwards towards the base of the posterior leaf : the second or central leaflet extends anteriorly beneath the anterior leaf but does not reach the median line. The ears are acutely pointed but lack a concavity in their posterior margins. The skull is short and broad, with a very wide rostrum and long pterygoids.

The *bicolor* group contains a high proportion of monotypic species, with only *ater*, *bicolor*, *galeritus* and *caffer* of widespread distribution and divisible into a number of clearly defined subspecies while *fulvus* and *cineraceus* are each divisible into two subspecies but are much less widely distributed. The remaining species are monotypic and while this may in part be due to the inadequacy of collections, there seems little doubt that this feature, with their sharply distinct morphological separation from each other in many cases and their restricted distribution, is an indication that some at least are relict forms that have survived the competition of the more successful species either by considerable specialization or in restricted habitats. Predominantly Indo-Australian in distribution, in Africa the group has rarely given rise to such highly specialized forms as *pygmaeus*, *coxi* and *papua*, and apart from *jonesi* forms a more closely related aggregation of species than those of the Indo-Australian region. However, the African representatives of the group have been isolated for a considerable period as is demonstrated by the great development of the noseleaf of *jonesi* when compared with that of *ridleyi* and by the structural differences in the posterior noseleaf and skull of *caffer* and its allies with those of *galeritus* and its associated species. Lack of diversity might be expected on a large land mass such as Africa : the island habitats of Indo-Australia have evidently encouraged diversification and have enabled species such as *dyacorum*, *sabanus*, *obscurus*, *pygmaeus*, *coxi* and *papua* to survive.

Hipposideros bicolor (Temminck), 1834, appears to be the first identifiable name in the group and is therefore adopted as the group name. Lesueur & Petit, in Péron, Voyage de Découvertes aux Terres Australes, Atlas, 1807, pl. 35 (volume not dated, date taken from Sherborn (1925 : 1661) : discussed by Oey & Feen (1958 : 230)) figured three bats from Timor under the name Rhinolophe Cruménifère (*Rhinolophus crumeniferus* N.). The status of this name has been discussed by Tate (1941 : 367 (footnote), 382), Laurie & Hill (1954 : 56) and Oey & Feen (loc. cit.). It is usually ascribed to Péron, the author of the text of the Voyage de Découvertes aux Terres Australes : however *Rhinolophus crumeniferus* is based solely on plate 35 of the Atlas, the title page of which clearly attributes this part of the work to Lesueur & Petit. Tate (1941 : 382) considered the plate to depict bats of the genus *Hipposideros* " probably related to *galeritus* and *cervinus* " while Laurie & Hill (loc. cit.) concluded that the bats represented were most nearly allied to *cervinus* (here considered to be a race of *H. galeritus*), an opinion supported by Oey & Feen (loc. cit.). The plate by Lesueur & Petit portrays bats with broad, triangular ears, which have a concavity in their posterior margins and with two lateral supplementary leaflets, thus referable to the *bicolor* group. The ears, however, are not noticeably covered with body fur. The anterior noseleaf is simple and the internarial septum is not inflated while the posterior leaf is high, supported by three well-defined septa not quite reaching the upper edge of the leaf, which is semicircular in outline. The leaf is largely unpigmented and there is a large frontal sac. It seems likely, therefore, that the three bats depicted by Lesueur & Petit represent *H. galeritus cervinus* or a closely related form. Tate (1941 : 387) postulates affinity with *H. papua* but the second leaflet shown in the plate by Lesueur & Petit does not extend forward beneath the anterior part of the horseshoe and these authors portray no incipient third leaflet. Pending discovery of the type or the collection of topotypes, the name must remain *incertae sedis*.

The species here allocated to the *bicolor* group (with the exception of *coronatus*, which from its description is evidently near to *calcaratus*, and *doriae*, probably synonymous with *sabanus*) may be keyed :

1 Lateral supplementary leaflets none or one 2
Lateral supplementary leaflets two or three 14

2 Anterior upper premolar (pm^2) obsolescent or obsolete, if present minute, extruded from toothrow, with second upper premolar (pm^4) and canine in contact, anterior lower premolar (pm$_2$) one quarter the length and one third or less the height of the second lower premolar (pm$_4$) 3
Anterior upper premolar (pm^2) present, never minute, anterior lower premolar (pm$_2$) one third or more the length and height of second lower premolar (pm$_4$) . 4

3 Anterior leaf without a median emargination : posterior leaf supported by a well-defined median septum and weaker lateral septa : pterygoids long, sphenoidal bridge wide . . . . *dyacorum* (p. 43)
Anterior leaf with well-defined median emargination : posterior leaf lacking supporting septa : pterygoids short, sphenoidal bridge narrow . *sabanus* (p. 44)

4 Internarial septum expanded to form a more or less disc-like structure between the nostrils : one lateral supplementary leaflet, sometimes rudimentary 5
Internarial septum not greatly expanded or modified, more or less parallel sided : no lateral supplementary leaflets 7

5 Internarial septum expanded to form a concave sub-circular disc . . . 6
Internarial septum expanded to form an ellipsoidal structure . *marisae* (p. 48)

6 Posterior leaf low, rounded above : lateral supplementary leaflet incipient, barely visible : palation U-shaped, without a post-palatal spicule . . *ridleyi* (p. 39)
Posterior leaf high, sub-triangular above : lateral supplementary leaflet well developed, extending anteriorly beneath anterior leaf to median line : palation square, with a small post-palatal spicule . . . . . . *jonesi* (p. 40)

7 Interorbital region wide, not sharply constricted, its width nearly equal to that of the rostrum 8
Interorbital region decidedly constricted, its width considerably less than that of the rostrum 9

8 Sphenoidal bridge well developed, broad, partially concealing small, elongate lateral apertures : well developed sphenoidal depression . . *calcaratus* (p. 37)
Sphenoidal bridge narrow, not concealing large, rounded lateral apertures : poorly developed sphenoidal depression . . . . *cupidus* (p. 38)

9 Anterior leaf without a median emargination : posterior leaf with three supporting septa : no glandular ridge on muzzle beneath margin of anterior leaf . . 10
Anterior leaf with small median emargination : posterior leaf without supporting septa : a low glandular ridge on muzzle beneath margin of anterior leaf *obscurus* (p. 47)

10 Internarial septum thickened and bulbous : anterior half of zygomata slender . 11
Internarial septum uninflated : anterior half of zygomata massive . . . 12

11 Superior projection of zygomata lacking or poorly developed : anterior upper premolar (pm^2) not extruded from toothrow . . . . . *cineraceus* (p. 35)
A low superior zygomatic projection : anterior upper premolar (pm^2) extruded or partially extruded from toothrow . . . . *ater* (p. 30)

12 Posterior projecting portion of vomer blade-like 13
Posterior projecting portion of vomer thickened . . . . . *bicolor* (p. 25)

13 Anterior lower premolar (pm$_2$) much reduced, one third the length of second lower premolar (pm$_4$) . . . . *fulvus* (p. 33)
Anterior lower premolar (pm$_2$) less reduced, one half the length of second lower premolar (pm$_4$) . . . . *nequam* (p. 36)

14 Anterior lateral supplementary leaflet extending anteriorly beneath anterior leaf to the median line 15
Anterior lateral supplementary leaflet not extending anteriorly beneath anterior leaf to the median line 16
15 Noseleaf not excessively specialized : intermediate leaf without a median eminence: posterior leaf supported by three septa of equal width, not deeply pocketed *pygmaeus* (p. 49)
Noseleaf greatly specialized : intermediate leaf with prominent median eminence : posterior leaf supported by narrow median septum and two broad lateral septa, deeply pocketed . . . . *coxi* (p. 68)
16 Second lateral supplementary leaflet not extending anteriorly beneath the anterior leaf : no trace of a third leaflet 17
Second lateral supplementary leaflet extending anteriorly beneath the anterior leaf : an incipient third leaflet . . . . *papua* (p. 70)
17 Posterior leaf having a transverse supplementary structure with a serrated upper edge developed from its posterior face 18
Posterior leaf without a transverse supplementary structure developed from its posterior face or with such a structure low, undeveloped and lacking a serrated upper edge 19
18 Anterior upper premolar (pm^2) small, slightly extruded from toothrow, or compressed between canine and second upper premolar (pm^4) . . *caffer* (p. 62)
Anterior upper premolar (pm^2) minute, extruded from toothrow, canine and second upper premolar (pm^4) in contact or nearly so . . . . . *beatus* (p. 66)
19 Posterior leaf supported by three septa 20
Posterior leaf without supporting septa, paired low lateral ridges sometimes present *fuliginosus* (p. 61)
20 Internarial septum not expanded : pterygoids long, sphenoidal bridge wide, partially concealing lateral apertures 21
Internarial septum expanded to form a slightly disc-like structure : pterygoids short, sphenoidal bridge narrow, not concealing lateral apertures . *curtus* (p. 60)
21 Ears haired for one half of their length : tips of upper incisors strongly convergent *breviceps* (p. 58)
Ears haired for two thirds of their length : tips of upper incisors not strongly convergent . . . . *galeritus* (p. 52)

Hipposideros bicolor

The ears are large and rounded, their anterior margins strongly convex and their posterior margins lacking any concavity just behind the tip. There is a distinct antitragal fold. The noseleaf is simple, of moderate size, and lacks lateral supplementary leaflets. The internarial septum is more or less triangular, broad at the base, narrowed between the nostrils, very slightly inflated and separated from the lateral parts of the anterior leaf by deep grooves. The lateral parts of the anterior leaf adjacent to the nostrils are not expanded and do not partially conceal the narial openings. The intermediate part of the leaf is unspecialized and the posterior leaf is supported by three septa. The skull is elongate and slender, with a comparatively broad braincase, narrowed interorbital region and slightly inflated rostral eminences. There is a low sagittal crest. The zygomata are massive, with or without a low superior jugal projection, and the anteorbital foramina are rather elongats, closed by a narrow bar of bone. The premaxillae are narrow and taken together make a wedge-shaped junction with the maxillae. Their anterior enclosing processes are delicate and do not enclose the rounded anterior palatal foramina. The palation is shallowly V-shaped and the mesopterygoid fossa is wide, with a projecting, thickened vomer. The pterygoids are long and the sphenoidal bridge wide, partially concealing large, elongate lateral apertures. There is a shallow oval sphenoidal depression and the cochleae are of moderate size, their width a little greater than their distance apart. The anterior upper premolar (pm^2) is very small and is extruded from the toothrow, while the posterior ridge of the third upper molar is reduced to approximately one half of the length of the anterior ridge. The crown area of the outer lower incisors is equal to that of the inner lower incisors or is very slightly greater, while the anterior lower premolar (pm_2) is one half or more the length of the second lower premolar (pm_4) and two thirds to three quarters its height.

Andersen (1918 : 379) provided the first study of the group of species allied to *Hipposideros bicolor*, recognizing among others a small species, *H. cineraceus*, a species of medium size, which he called *H. bicolor* and two larger species, *H. pomona* and *H. gentilis* (here considered to be conspecific) in southeastern Asia. Tate (1941 : 360), however, in the course of revisionary work on the genus, has designated a lectotype for *Rhinolophus bicolor* Temminck, 1834, and has left its exact application in some doubt. The original description by Temminck, 1834, Tijdschr. Natuur. Gesch. **1** (1) : 19, pl. 1, fig. 3 listed no specimens, but Temminck stated that the species was to be found in Java, Amboina and Timor and said that it had been received in considerable numbers at the Netherlands Museum. Later, Temminck, 1835, Monogr. Mamm. **2** : 18 (which Tate apparently thought to be the original description) provided a further, more detailed description, basing it on the examination of ten females and four males, and giving as the provenance of the species the islands of Java, Amboina and Timor. His series is clearly composite, the specimens from Amboina, which Temminck said to be smaller than those from Java being referable to the form subsequently described by Peters (1871a : 323) as *Phyllorhina amboinensis*. Temminck gives measurements of an adult from Java with forearm " 1 pouce 8 lignes " (approximately 43 mm.), perhaps a representative of *H. bicolor* in the sense of Andersen (1918 : 380), a species of medium size widely distributed in the Indo-Australian region.

Jentink (1887 : 272, 1888 : 168) has listed among other specimens in the collections of the Rijksmuseum van Natuurlijke Historie, Leiden, a large part of the series probably forming the basis of the description of *Rhinolophus bicolor* by Temminck. Tate (1941 : 361) has examined these specimens and has designated as lectotype specimen " d " of Jentink (1888 : 168), collected by Van Hasselt (from the collections of Kuhl and Van Hasselt according to Jentink) on the Côte d'Anjer, in the extreme northwest of Java, whence Tate restricts the type locality. This selection introduces a change of name into the group as originally defined by Andersen (1918 : 379) since from the detailed notes on the lectotype provided by Tate, it is evidently a member of the species called *Hipposideros gentilis* by Andersen (1918 : 380), considered by Ellerman & Morrison-Scott (1951 : 127) and in the present study to be conspecific with *H. pomona*, also proposed by Andersen in this work. *Rhinolophus bicolor* Temminck is by far the earliest name in this section of the genus and as a result must replace *H. pomona* as used by Andersen (1918 : 380) and some subsequent authors. The earliest name identifiable with certainty for the species of medium size called *H. bicolor* by Andersen (1918 : 380) appears to be *Hipposideros ater* Templeton, 1848.

APPROXIMATE DISTRIBUTION : India east to Hainan and the Philippine Islands ; Malay Peninsula, Sumatra, Java and adjacent islands.

Hipposideros bicolor bicolor (Temminck)

Rhinolophus bicolor Temminck, 1834 : 19, pl. 1, fig. 3 ; 1835 : 18 (further description). Lectotype designated and type locality restricted to Anjer coast, northwestern Java by Tate (1941 : 361).

Hipposideros javanicus Sody, 1937 : 215. Babakan, Kroja, Tjilatjap, central Java.

No Javan specimens are available for study : from Tate (1941 : 361) the lectotype has an elongate skull with slight nasal eminences and a rather pronounced posterior interparietal swelling. The anterior upper premolar (pm^2) is slightly extruded from the toothrow, while the anterior lower premolar (pm_2) is three quarters the height of the second lower premolar (pm_4). Tate suggested that *Hipposideros javanicus* Sody, 1937 might be synonymous with *H. b. bicolor* as represented by the lectotype in Leiden. The measurements of the type specimen of *H. javanicus* as quoted by Sody agree closely with those of the lectotype of *H. b. bicolor* as recorded by Tate.

DISTRIBUTION : Java ; Banka Island.

Hipposideros bicolor pomona Andersen

Hipposideros pomona Andersen, 1918 : 380. Haleri, north Coorg, India.

The zygomata have a low jugal projection and the anterior upper premolar (pm^2) is very small while the anterior lower premolar (pm_2) is one half the length and two thirds the height of the second lower premolar (pm_4).

DISTRIBUTION : Southern India.

Hipposideros bicolor gentilis Andersen

Hipposideros gentilis Andersen, 1918 : 380. Thayetmyo, Burma.

Cranially similar to *H. b. pomona* but the zygomata lack a definite jugal projection. The anterior lower premolar (pm_2) is slightly more than one half the length and two thirds the height of the second lower premolar (pm_4).

DISTRIBUTION : Northern India ; Assam ; Sikkim ; Burma.

Hipposideros bicolor sinensis Andersen

Hipposideros gentilis sinensis Andersen, 1918 : 380. Foochow, Fukien, China.

The anterior lower premolar (pm$_2$) is three quarters or more the length of the second lower premolar (pm$_4$), sometimes almost equal to it in length, and is two thirds its height. Cranially, the subspecies otherwise resembles *H. b. gentilis*. Osgood (1932 : 221) suggested that *H. b. sinensis* may be a synonym of *H. b. gentilis*, while Bourret (1942b : 11) considered that *H. b. sinensis* was not a valid subspecies.

DISTRIBUTION : Southern China ; Hainan ; recorded from Hong Kong by Romer (1960 : 2) ; Siam (part) ; Indochina (recorded as *H. gentilis* by Osgood (1932 : 220) and Bourret (1942b : 11 ; 1944 : 6)).

Hipposideros bicolor atrox Andersen

Hipposideros gentilis atrox Andersen, 1918 : 380. Semangko Gap, Selangor, Federation of Malaya, 2,800 feet.

There is a low jugal projection on the zygomata and the sphenoidal pits are very elightly wider than in the foregoing subspecies. The anterior lower premolar (pm$_2$) is one half or less the length and one half the height of the second lower premolar (pm$_4$). Davis (1961 : 90) gives a description, with measurements, of a series of *H. b. atrox* from the Federation of Malaya.

DISTRIBUTION : Malay Peninsula ; Terutau Island ; Tioman Island ; Sumatra.

Hipposideros bicolor major Andersen

Hipposideros gentilis major Andersen, 1918 : 380. Bua-Bua, Engano Island, off west coast of Sumatra.

Cranially exactly like *H. b. atrox* with the anterior lower premolar (pm$_2$) one half the length and height of the second lower premolar (pm$_4$). Although Andersen in the original description stated that *H. b. major* was larger than *H. b. atrox*, the two subspecies seem likely to prove synonymous.

Hipposideros bicolor erigens Lawrence

Hipposideros erigens Lawrence, 1939 : 56. Lower slopes of Mount Halcon, northern side, near Calapan, Mindoro, Philippine Islands.

There are no specimens of this form in the collections of the British Museum (Natural History). Its large size, large ears, noseleaf, bullae and teeth suggest alliance with *H. bicolor*.

Hipposideros bicolor macrobullatus Tate

Hipposideros bicolor macrobullatus Tate, 1941 : 357. Talassa, near Maros, south Celebes, 300 metres.

There are no specimens of this form in the collections of the British Museum (Natural History). Its measurements and characters as given by Tate agree closely with those of *H. bicolor*.

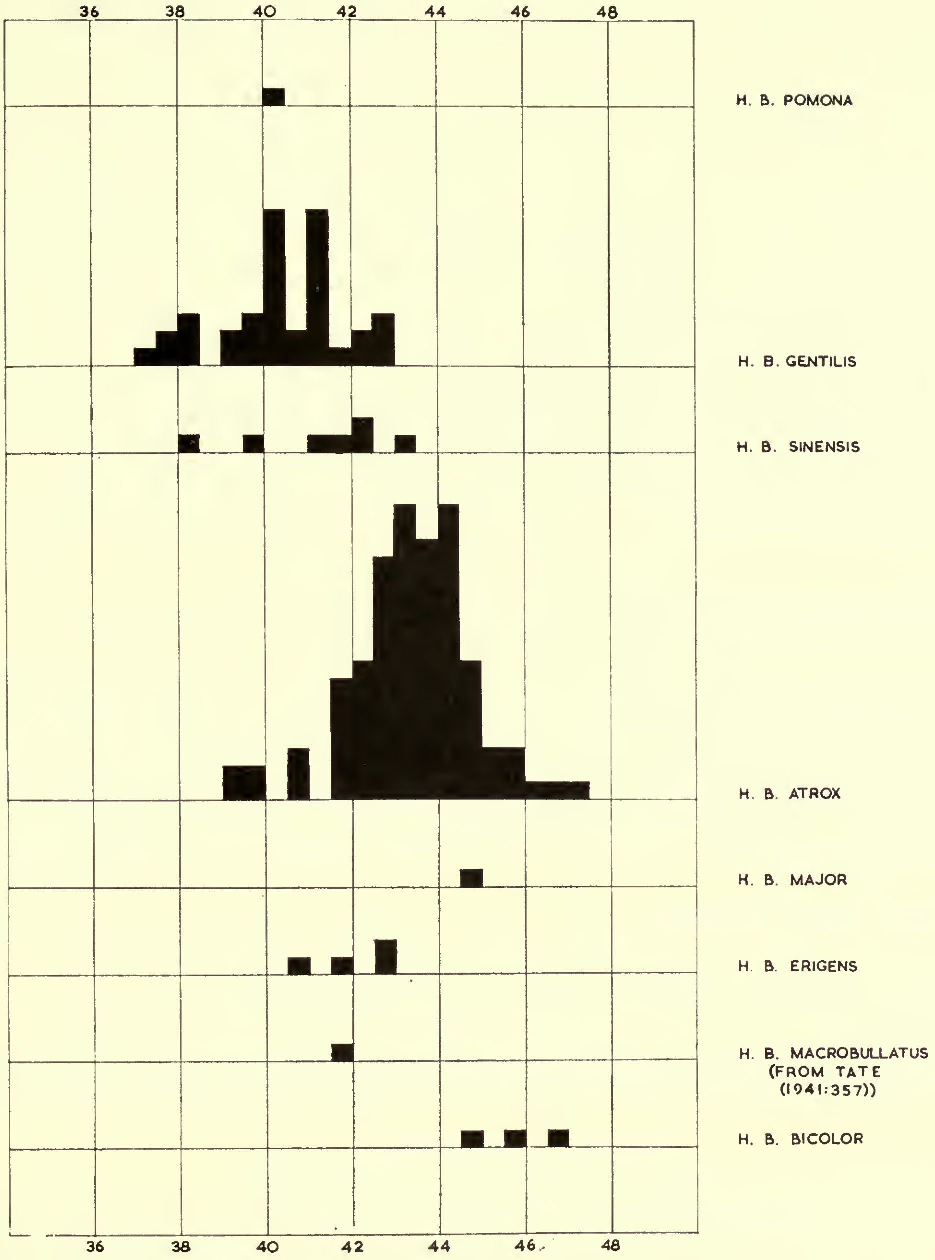


FIG. 4. Length of forearm in *Hipposideros bicolor*

Hipposideros ater

The ears and noseleaf are very much like those of *H. bicolor* but the internarial septum is swollen and inflated, slightly bulbous, narrow at its upper end and separated from the lateral parts of the anterior leaf by deep grooves. The narial margins of the anterior part of the leaf are expanded and partially conceal the nostrils. Cranially, there is considerable similarity to *H. bicolor* but the zygomata are slender anteriorly and the vomer projects slightly into the mesopterygoid fossa and is slightly thickened. The anterior upper premolar (pm^2) is usually extruded from the toothrow and the posterior ridge of the third upper molar is one half or less the length of the anterior ridge. The outer lower incisors are very slightly larger in crown area than the inner lower incisors. The anterior lower premolar (pm_2) varies in length from one half or less of the length of the second lower premolar (pm_4) in western subspecies to a length almost equal to that of the second lower premolar in eastern subspecies, while its height is one half to two thirds that of the second lower premolar. Formerly known as *H. bicolor*, this species must now be called *H. ater* since the designation of a lectotype for *Rhinolophus bicolor* Temminck by Tate (1941 : 361) transfers that name to the species formerly called *H. pomona* or *H. gentilis*.

DISTRIBUTION : India to the Philippine Islands, Papua and northern Australia.

Hipposideros ater ater Templeton

Hipposideros ater Templeton, 1848 : 252. Colombo, Ceylon.
Hipposideros atratus Kelaart, 1850a : 208. Substitute for *ater*.

The zygomata have a well developed jugal projection and the posterior ridge of the third upper molar is greatly reduced and obsolescent. The anterior lower premolar (pm_2) is less than one half the length of the second lower premolar (pm_4) and its height is one half or less than that of the second lower premolar. There appears to be no difference between specimens from Peninsular India (called *Hipposideros* (?) *bicolor fulvus* by Ellerman & Morrison-Scott (1951 : 127)) and those from Ceylon.

DISTRIBUTION : Ceylon ; India.

Hipposideros ater nicobarulae Miller

Hipposideros nicobarulae Miller, 1902 : 781. Little Nicobar Island, Bay of Bengal.

Similar to *H. a. ater* but slightly larger, with the anterior lower premolar (pm_2) one half the length of the second lower premolar (pm_4) and one half or less its height.

Hipposideros ater saevus Andersen

Hipposideros albanensis saevus Andersen, 1918 : 380. Kei Islands.
Hipposideros gentilis toala Shamel, 1940 : 352. Toeare, Celebes.

Very similar to *H. a. ater* but a little larger, with the jugal projection of the zygomata very low or lacking. The anterior lower premolar (pm_2) varies from slightly more than one half the length to three quarters the length of the second lower premolar (pm_4), and is one half or slightly more its height.

Andersen (1918 : 380) employed *Rhinolophus bicolor* Temminck, 1834, for a medium sized (forearm 37–42 mm.) species of bat of his *bicolor* group, giving as its provenance Sumatra and Java. In this he was followed by a number of subsequent authors including Chasen (1940 : 44), Ellerman & Morrison-Scott (1951 : 126) and Laurie & Hill (1954 : 54). However, Tate (1941 : 361) has designated as lectotype of *Rhinolophus bicolor* Temminck a specimen from that part of the original series still extant in the Rijksmuseum van Natuurlijke Historie, Leiden. It is obvious from the notes and measurements of the lectotype as quoted by Tate that this specimen is not representative of the species of *Hipposideros* hitherto called *bicolor*. It is a large bat in comparison with the species formerly called *bicolor*, with a forearm of 47 mm., zygomatic width 9·1 mm., greatest mastoid width 9·4 mm., least interorbital width 3·0 mm. and c–m^3 6·5 mm. Tate also points out that *Hipposideros javanicus* Sody, 1937, from Java, is very probably synonymous with the species represented by this lectotype. These factors taken in conjunction indicate that the lectotype designated by Tate belongs to the species called *gentilis* by Andersen (1918 : 380) and subsequent authors, and *Rhinolophus bicolor* Temminck, 1834, must therefore be transferred to this species. This leaves the bats from Java and its environs, hitherto called *H. bicolor bicolor*, without a name, and in the ordinary course of events a new subspecific term would be required. However, there seems little to distinguish these bats from *H. ater saevus* : specimens from Java, Sumatra and the Malay Peninsula average very slightly smaller than those from more easterly localities and are a little paler while the anterior lower premolar (pm_2) is slightly more reduced, but these points scarcely seem to warrant subspecific recognition.

Shamel (1940 : 352) described *Hipposideros gentilis toala*, a Celebesian bat which he considered related to the mainland species *gentilis* (=*bicolor* in the present sense). However, Tate (1941 : 361, 390) thought *toala* a probable synonym of *H. a. saevus* : there seems in fact to be little size difference between *toala* and *saevus* (measurements of the type specimen of *toala* as quoted by Tate (1941 : 361) conflict with those given by Shamel in the original description) and in the present study they are considered to be synonymous.

DISTRIBUTION : Mergui Archipelago ; Tenasserim ; Peninsular Siam ; Condor Island ; Federation of Malaya ; Teratau Island ; Tioman Island ; Sumatra ; Java ; Bali ; Celebes ; Peleng Island ; Kei Island ; Buru ; Ceram ; possibly also Sanghir and Talaud Islands. Tate (1941 : 362) states that a specimen in the American Museum of Natural History from Halmahera is identical with one from Java in the Museum of Comparative Zoology, which from the measurements quoted by Tate is apparently an example of *H. ater*.

Hipposideros ater antricola (Peters)

Phyllorhina antricola Peters, 1861 : 709. Paracali, Luzon, Philippine Islands.

Hipposideros wrighti Taylor, 1934 : 237. Baguio, Benguet (near Headwaters gold mine), Luzon, Philippine Islands.

A specimen from Balabac Island (B.M. 94.7.2.51) is referred to this subspecies. It has the anterior lower premolar (pm_2) considerably reduced, one half the length and height of the second lower premolar (pm_4). Lawrence (1939 : 55) summarizes the taxonomic history of *Hipposideros wrighti* Taylor and concludes that it may be in fact a re-description of *H. a. antricola.*

DISTRIBUTION : Philippine Islands : Luzon ; Marinduque ; Mindoro ; Mindanao (Sanborn (1952 : 104)) ; Palawan (Sanborn (1952 : 104)) ; Balabac.

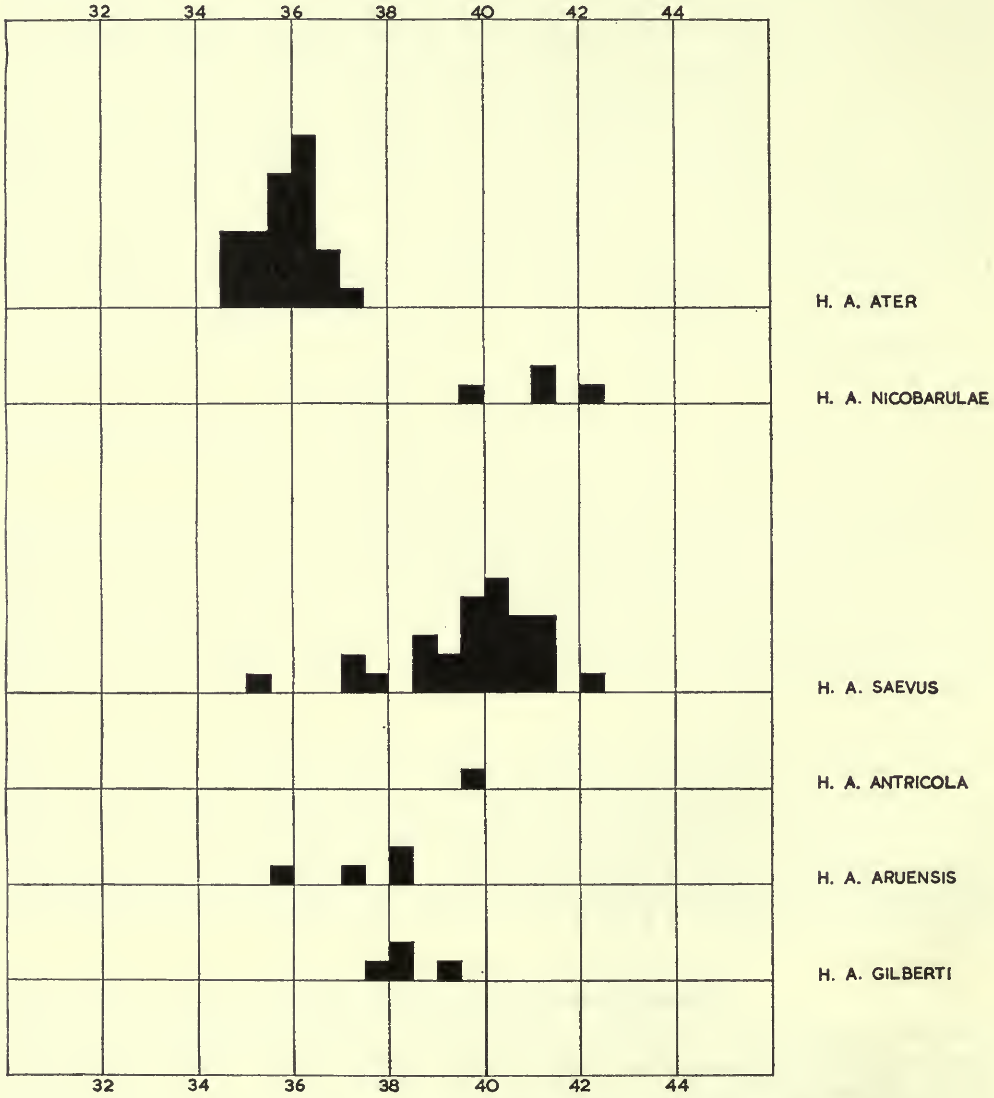


FIG. 5. Length of forearm in *Hipposideros ater*

Hipposideros ater aruensis Gray

Hipposideros aruensis Gray, 1858 : 107. Aru Islands.
Hipposideros albanensis Gray, 1866b : 220. Port Albany, northwest Queensland.

The zygomata bear a small jugal projection while the anterior lower premolar (pm_2) is rather larger than in *H. a. saevus* and is equal or almost equal in length to the second lower premolar (pm_4) and is two thirds its height. The type specimen is the only available example of *Hipposideros albanensis* Gray. Its skull is fragmentary and only the left-hand maxillary toothrow and the mandible remain. The dentition is identical with that of *H. a. aruensis*.

DISTRIBUTION : Aru Islands ; southern and northwestern New Guinea ; northern Queensland.

Hipposideros ater amboinensis (Peters)

Phyllorhina amboinensis Peters, 1871a : 323. Amboina.

There is no example of this subspecies in the collections of the British Museum (Natural History). It is very probably synonymous with *H. a. aruensis* (see Tate (1941 : 380)).

Hipposideros ater gilberti Johnson

Hipposideros bicolor gilberti Johnson, 1959 : 183. Oenpelli, East Alligator River, Northern Territory, Australia (12° 21′ S., 133° 04′ E.).

The collections of the British Museum (Natural History) contain four topotypes (B.M. 23.5.14.9–12) of this subspecies. They agree closely with the description and measurements given by Johnson : there seems little to distinguish them from *H. a. aruensis* except their slightly paler colour.

Hipposideros fulvus

The ears are very large and rounded, longer than the head, the upper third of their posterior margins very slightly flattened. The noseleaf closely resembles that of *H. bicolor* and has the internarial septum narrow, uninflated, broadened at its base and narrowed between the nostrils. The narial margins of the anterior leaf are not expanded, and the nostrils are clearly visible. The skull is elongate and comparatively slender, with a low to moderate sagittal crest and uninflated rostral eminences. The zygomata are broad, with a moderate jugal projection. The premaxillae are like those of *H. bicolor* but make a more rounded, less wedge-shaped junction with the maxillae. The palation is more or less V-shaped, with long pterygoids, wide mesopterygoid fossa and a very thin, blade-like projecting vomer. The cochleae are of moderate size, their width a little greater than their distance apart. There is an ovate sphenoidal depression. The anterior upper premolar (pm^2) is minute, extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact or nearly so. The third upper molar is reduced, its posterior ridge one quarter or less the length of the anterior ridge. The outer lower incisors are slightly larger in crown area than the inner lower incisors. The anterior lower premolar (pm_2) is much reduced and is from one quarter to one third the length and one quarter to one half the height of the second lower premolar (pm_4). *Hipposideros fulvus* may be distinguished from *H. bicolor* and *H. ater* by its larger ears : from *H. bicolor* by its blade-like vomer and much reduced anterior lower premolar and from *H. ater* by its uninflated internarial septum and broadened zygomata.

DISTRIBUTION : India east to Tonkin and Annam ; Lower Siam.

Hipposideros fulvus fulvus Gray

Hipposideros fulvus Gray, 1838 : 492. Dharwar, India.
Hipposideros murinus Gray, 1838 : 492. Dharwar, India.
Rhinolophus murinus Elliot, 1839 : 99. Dharwar, India. (Re-description of *Hipposideros murinus* Gray, 1838, perhaps based on the same original material.)
Rhinolophus fulgens Elliot, 1839 : 99. Dharwar, India. (Re-description of *Hipposideros fulvus* Gray, 1838, perhaps based on the same original material.)
Phyllorhina aurita Tomes, 1859b : 76. India.

Hipposideros fulvus fulvus occurs in two colour phases : one chestnut brown above and below, the other with the dorsal surface dark brown, the hairs with paler bases and with the ventral surface rather paler than the back. The two colour phases furnish the basis of the names *Hipposideros fulvus* and *Hipposideros murinus* proposed by Gray and likewise of *Rhinolophus fulgens* and *Rhinolophus murinus* proposed by Elliot. This fact was recognized by Wroughton (1912a : 829, 1912b : 1179) who first realized that the descriptions by Elliot most probably related to the bats described by Gray. The type locality of both *Hipposideros fulvus* Gray and *Hipposideros murinus* Gray is given by their describer as Madras. This appears to be an error for Dharwar, whence Elliot obtained the original specimens. Brosset (1962 : 613) has studied the biology of *H. fulvus* and gives measurements and notes on its colour variation.

Tomes in describing *Phyllorhina aurita* failed to compare it in detail with any *Hipposideros* of the *bicolor* type hitherto described from India. His type specimen agrees closely with *H. fulvus*.

DISTRIBUTION : Ceylon ; Peninsular India (on west coast north to Bombay) ; Bengal, Bhutan Duars ; Sikkim ; Assam ; Burma ; Tenasserim ; Lower Siam ; Tonkin ; Annam.

Hipposideros fulvus pallidus Andersen

Hipposideros fulvus pallidus Andersen, 1918 : 381. Junagadh, Kathiawar, India.

This subspecies differs from *H. f. fulvus* only in its paler back and underparts, the ventral surface being creamy, faintly tinged with grey and lacking all trace of brown.

DISTRIBUTION : Kathiawar ; Gwalior ; Bihar and Orissa ; Sind ; Cutch ; Rajputana ; Baluchistan.

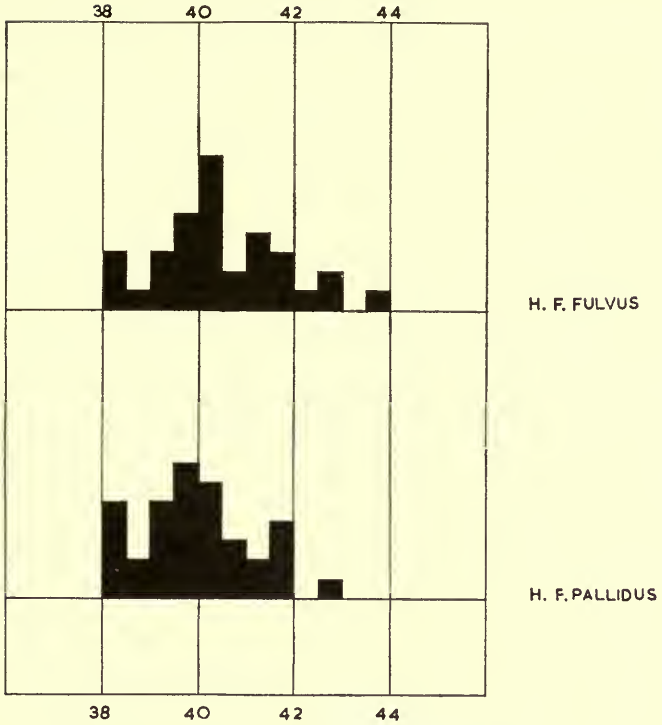


FIG. 6. Length of forearm in *Hipposideros fulvus*

Hipposideros cineraceus

The ears are large and rounded and are similar to those of *H. fulvus*. The noseleaf is similar to that of *H. bicolor*, the internarial septum more or less parallel-sided, inflated and bulbous, with the narial margins of the anterior leaf expanded to partially conceal the nostrils. The skull is comparatively small, with an inflated braincase, low sagittal crest, narrow interorbital region and slightly inflated rostral eminences. The zygomata are narrow and delicate and lack a jugal projection. The premaxillae resemble those of *H. bicolor* and make a wedge-shaped junction with the maxillae. The palation is V-shaped and the mesopterygoid fossa wide, with slightly flared pterygoids. The vomer projects into the mesopterygoid fossa and is thickened posteriorly. The anterior upper premolar (pm^2) is small, compressed between the canine and the second upper premolar (pm^4) but not markedly extruded from the toothrow. The posterior ridge of the third upper molar is one third to one half the length of the anterior ridge. The outer lower incisors are a little larger in crown area than the inner lower incisors. The anterior lower premolar (pm_2) is reduced to a little more than one half the length and height of the second lower premolar (pm_4). The small size of *H. cineraceus* readily distinguishes it from its associated species, except perhaps from *H. ater* : it may be distinguished from this species by its slender, slightly smaller skull, with delicate zygomata which lack a jugal projection, and its less reduced, unextruded anterior upper premolar. It occurs in two colour phases, the one brownish, the other a brighter, redder phase.

DISTRIBUTION : Northern India west to the Punjab ; Assam ; Burma ; Siam ; Tonkin ; Malay Peninsula ; Riau Archipelago ; Anamba Islands ; Borneo.

Hipposideros cineraceus cineraceus Blyth

Hipposideros cineraceus Blyth, 1853 : 410. Near Pind Dádan Khan, Salt Range, Punjab.

DISTRIBUTION : as above, except perhaps for the foothills of the Himalayas.

Hipposideros cineraceus micropus (Peters)

Phyllorhina micropus Peters, 1872 : 256. Dehra Dun, near Simla, northwestern India.

The type specimen is the only available example of *H. c. micropus*. Its skull is smaller in some respects than the skull of *H. c. cineraceus* and it may represent a northern race.

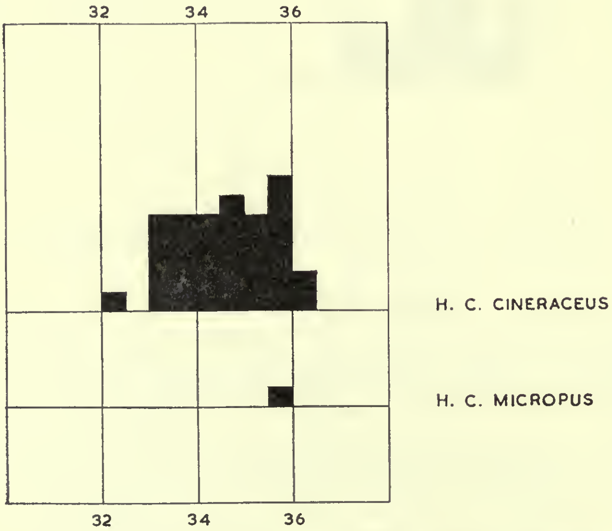


FIG. 7. Length of forearm in *Hipposideros cineraceus*

Hipposideros nequam Andersen

Hipposideros nequam Andersen, 1918 : 381. Klang, Selangor, Federation of Malaya.

The type specimen appears to be the only known example of *H. nequam*. The original description is very brief and no further diagnostic or comparative notes have appeared, although Tate (1941 : 386) noted its relationship to *H. bicolor* and pointed out (p. 362) that its greatly reduced anterior lower premolar (pm_2) separated it from *H. bicolor* with which the length of its forearm would otherwise place it. The ears are large and rounded, similar to those of *H. fulvus*, while the noseleaf is closely similar to that of *H. bicolor*, but is larger. The internarial septum is uninflated and the narial margins of the anterior leaf are not expanded. The skull of the type specimen is badly damaged and only part of the rostrum with both upper toothrows and the anterior part of the mandible remain. The rostral eminences are slightly inflated and the anteorbital foramen is large and rather elongate The premaxillae are short and broad, with delicate enclosing processes which do not encircle the anterior palatal foramina. They make a wedge-shaped junction with the maxillae. The palation is shallowly V-shaped and the mesopterygoid fossa is wide, with a projecting, blade-like vomer. The upper canines have a low posterior cusp, and the anterior upper premolar (pm^2) is small, not extruded from the toothrow, compressed between the canine and the second upper premolar (pm^4), which has a small anterior cusp. The posterior ridge of the third upper molar is reduced to one half the length of the anterior ridge. The outer lower incisors are very slightly larger in crown area than the inner lower incisors, while the anterior lower premolar (pm_2) is reduced to one half the length and height of the second lower premolar (pm_4). Cranially, *H. nequam* resembles *H. bicolor atrox* and is approximately the same size, but it differs from *H. bicolor* in its slightly more inflated rostral eminences, shorter, broader premaxillae, blade-like vomer and more greatly reduced anterior lower premolar (pm_2). Although the large ears, blade-like vomer and greatly reduced anterior lower premolar (pm_2) suggest a possible relation to *H. fulvus*, *H. nequam* is larger, with a broader rostrum, shorter, much broader premaxillae, which make a wedge-shaped and not rounded junction with the maxillae, wider mesopterygoid fossa and more massive dentition, the canine with a low posterior cusp and the second upper premolar (pm^4) with a small anterior cusp.

Hipposideros calcaratus (Dobson)

Phyllorhina calcarata Dobson, 1877 : 122. Duke of York Island.

The ears of *H. calcaratus* are broad and more or less triangular, their posterior margins with a slight concavity just behind the tip. There is a distinct internal fold. The noseleaf is simple, of medium size, without lateral supplementary leaflets and in general similar to that of *H. bicolor*, with the internarial septum uninflated and the narial margins of the anterior leaf not expanded. The posterior leaf is simple and unwidened, with an ill-defined median supporting septum, the lateral septa weak or absent. A frontal sac is present in both sexes. The skull is unspecialized, very little less elongate than that of *H. bicolor*, with an elongated, uninflated braincase, low sagittal crest, unconstricted interorbital region and slightly inflated rostral eminences. The zygomata are broad, with a well developed jugal projection, the zygomatic width greater than the mastoid width. The premaxillae are elongate and narrow, with delicate anterior enclosing processes which do not encircle the elliptical anterior palatal foramina. They make a U-shaped junction with the maxillae and the palation is shallowly V-shaped, with a wide mesopterygoid fossa and blade-like projecting vomer. The pterygoids are long and wide and the sphenoidal bridge is wide, partially concealing elongate lateral apertures between pterygoids and alisphenoids. There is a small oval or ovate sphenoidal depression and the width of the cochleae is approximately equal to their distance apart. The mandible is massive, with a substantial coronoid process and a heavy, knob-like angular process. The upper incisors are simple with their outer lobes almost obsolete. The upper canines are massive, with a well developed posterior cusp extending one third or more the length of the tooth. The anterior upper premolar (pm^2) is small, compressed between the canine and the second upper premolar (pm^4), sometimes partially extruded. The third upper molar has its posterior ridge one third or less the length of the anterior ridge. The outer lower incisors are equal in crown area to the inner pair. The anterior lower premolar (pm_2) is only slightly reduced, two thirds or more the length and three quarters the height of the second lower premolar (pm_4).

Tate (1941 : 358, 362) allocated *H. calcaratus* (Dobson) and *H. cupidus* Andersen to a *calcaratus* group distinct from his *bicolor* and *galeritus* groups. There seems to be no justification for this comparatively wide separation : *H. calcaratus* and *H. cupidus* are not greatly removed from *H. bicolor* and its allies and closely resemble them in the basic features of the ears, noseleaf and skull. They differ from *H. bicolor* and its associated species chiefly in their more triangular, less rounded ears, more simplified noseleaves and in having the interorbital region of the skull unconstricted.

DISTRIBUTION : New Guinea ; Bismarck Archipelago : Duke of York Island ; Solomon Islands : Russell ; New Georgia ; Nissan ; Rennell.

Hipposideros cupidus Andersen

Hipposideros cupidus Andersen, 1918 : 383. Eaga, Papua.

The original diagnosis is very brief : Tate (1941 : 362, 381, 382) and Hill (1956 : 77, 78) give supplementary notes. The ears and noseleaf are as in *H. calcaratus*. In its cranial characters *H. cupidus* is closely similar to *H. calcaratus*, but the zygomata have only a low jugal projection and the pterygoids and sphenoidal bridge are narrow, the sphenoidal bridge not partially concealing wide, rounded lateral apertures. The sphenoidal depression is very poorly developed. The dentition is closely similar to that of *H. calcaratus* but the canines are slender while retaining the high posterior cusp. *Hipposideros cupidus* is in general very similar to *H. calcaratus* and the two species are sympatric for part of their range. Tate (1941 : 362) studied series of both and formulated a key for their separation. Hill (1956 : 77, 78) on the basis of a re-examination of the type specimens commented on the diagnostic characters used by Tate and pointed out that criteria of size do not appear to be valid in the Solomon Islands and that the height of the posterior canine cusp is not a reliable diagnostic character.

DISTRIBUTION : New Guinea ; Japen Island ; Bismarck Archipelago : Duke of York Island ; Tabar Islands ; Solomon Islands : New Georgia ; Banika.

Hipposideros coronatus (Peters)

Phyllorhina coronata Peters, 1871a : 327. Mainit, Surigao, northeastern Mindanao, Philippine Islands.

There is no example of this species in the collections of the British Museum (Natural History). Its size, lack of lateral supplementary leaflets and unspecialized posterior leaf suggests affinity with *H. calcaratus*.

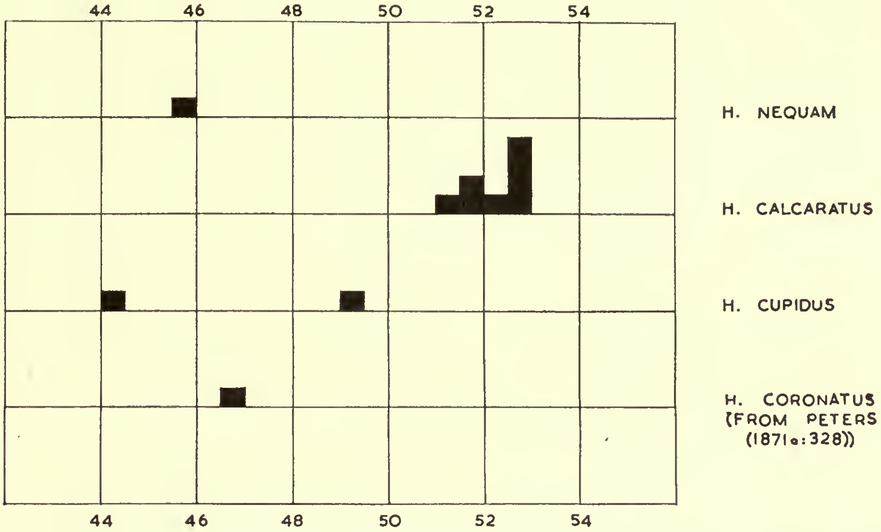


FIG. 8. Length of forearm in *Hipposideros nequam*, *H. calcaratus*, *H. cupidus* and *H. coronatus*

Hipposideros ridleyi Robinson & Kloss

Hipposideros ridleyi Robinson & Kloss, 1911 : 241. Botanic Gardens, Singapore Island.

Gibson-Hill (1949 : 191) believed the type specimen of *H. ridleyi* to be lost. However, in the course of the present study, it was found among a collection of bats sent many years ago to Andersen from the Federated Malay States Museum for study at the British Museum (Natural History). No further specimens appear to have been recorded. The ears are very large and broad, sub-triangular and bluntly pointed, their anterior margins convex, their posterior margins straight for the upper third and not concave. There is a well-developed fold at the antitragal lobe and the ears are haired for their basal quarter. The noseleaf is large, almost completely covering the muzzle and lacks lateral supplementary leaflets. A slight longitudinal swelling behind and parallel to the outer margin of the anterior leaf however, may represent an incipient leaflet. The anterior leaf is broad, with its narial margins slightly expanded and partially concealing the nostrils. The internarial septum is greatly expanded to form a concave circular disc between and anterior to the nostrils which however does not obscure the narial openings. The narial flaps or lappets are considerably developed to form a pocket encircling the nostrils, but do not rise above the level of the horseshoe. The intermediate part of the leaf is cushion-like, with a low median eminence. The posterior leaf is high, its upper edge semicircular, its lower half supported by three prominent septa of equal depth enclosing four deep pockets, its upper half smooth. The rear walls of the central pockets form a low projecting structure on the posterior face of the leaf. A frontal sac is present in the male type specimen.

The skull is comparatively large and elongate, with broad braincase, low sagittal crest, slight supraorbital ridges, narrow interorbital region, a very shallow frontal depression and slightly inflated rostral eminences. The zygomata are slender with a well developed jugal projection. The anteorbital foramen is elongate, closed by a moderate bar. The premaxillae are short and broad anteriorly, with short anterior enclosing processes. They are narrowed posteriorly to make a wedge-shaped junction with the maxillae and do not enclose the anterior palatal foramina. The palation is U-shaped, with a wide mesopterygoid fossa and a thin, blade-like projecting vomer. The pterygoids are long and wide with a wide sphenoidal bridge, partially concealing elongate lateral apertures. There is an ovate sphenoidal depression and the width of the cochleae is a little greater than their distance apart. The upper incisors are weakly bilobed, their tips strongly convergent and almost touching. The upper canines are slender, with well developed cingula. The anterior upper premolar (pm^2) is small, compressed between the canine and the second upper premolar (pm^4) and the posterior ridge of the third upper molar is one half the length of the anterior ridge. The outer lower incisors are very slightly greater in crown area than the inner lower incisors and the anterior lower premolar (pm_2) is nearly as long as the second lower premolar (pm_4) but only one half its height.

It is evident that *H. ridleyi* is closely related to *H. bicolor* and its immediately associated species, resembling them in having ears with a well developed internal fold, its lack of lateral supplementary leaflets and its narrow, elongate skull with broad brain case and zygomatic width less than the mastoid width. The curious specialization of the internarial septum appears to be a further development of the condition in *H. ater* and *H. cineraceus*, in which the internarial septum, although broadened and bulbous, has not developed an internarial disc or pad, and which tends towards *H. jonesi*, an African species exhibiting a yet more greatly developed internarial disc. This contention is supported by the parallel appearance in *H. ridleyi* of narial pockets and a deeply pocketed posterior leaf, structures found more greatly developed in *H. jonesi*.

Hipposideros jonesi Hayman

[Figure 9]

Hipposideros jonesi Hayman, 1947 : 71. Makeni, Sierra Leone, West Africa.

The ears are very large, broad, sub-triangular, with an acute point, their anterior margins slightly convex, their posterior margins very slightly so, with a faint concavity just behind the tip. There is a distinct internal fold at the antitragal lobe and the ears are haired for their basal third. The noseleaf is a greatly specialized structure with one well-developed lateral supplementary leaflet extending from the base of the intermediate part of the leaf anteriorly beneath the anterior leaf to the median line, with a deep emargination above the centre of the lip. The anterior leaf is broad, covering almost the entire width of the muzzle, with a faint anterior emargination. The internarial septum is greatly expanded into a large concave, more or less circular disc between and just anterior to the nostrils, which it partially conceals. The narial flaps or lappets form pockets enclosing the nostrils and rise above the level of the anterior leaf. The intermediate part of the leaf is elevated but is otherwise unspecialized. The posterior leaf is high, its outline sub-triangular, with a blunt, rounded point, its lower half supported by a shallow median septum and two deeper lateral septa, forming three deep pockets, the central pocket larger than the lateral pockets and divided by the lower median septum. The posterior walls of the pockets do not form a projecting structure on the posterior face of the leaf and the upper half of the leaf is smooth. The frontal sac is very poorly developed in male specimens and lacking in female examples.

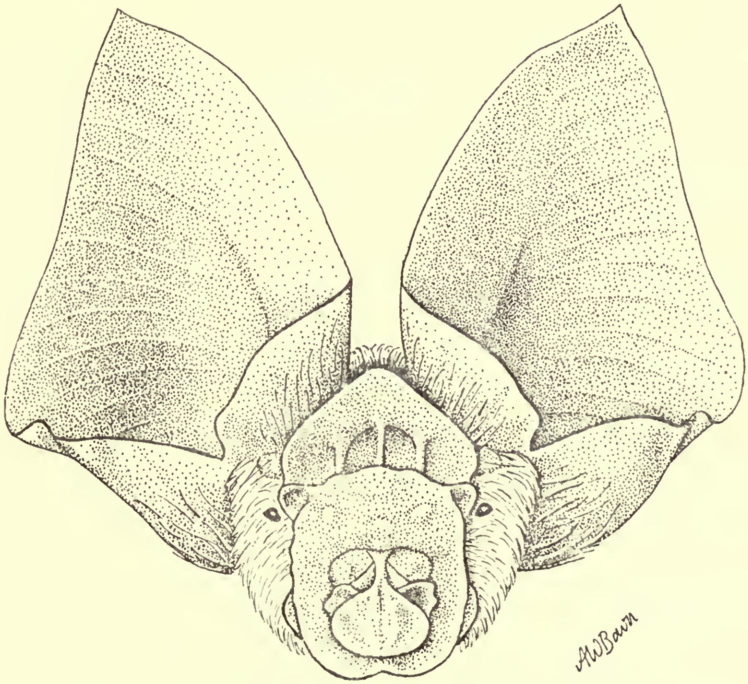


FIG. 9. *Hipposideros jonesi* ♀ (Type B.M. 47.629) (x3)

The skull is of medium size and is elongate with a broad braincase, low sagittal crest, barely definable supraorbital ridges, narrowed interorbital region and rostrum, with a shallow frontal depression and well-inflated rostral eminences. The rostrum is elongate, the premaxillae projecting beyond the canines. The zygomata are slender, with a low jugal process, and the zygomatic width is considerably less than the mastoid width. The anteorbital foramen is rounded and closed by a narrow bar. The premaxillae are broad anteriorly with delicate anterior enclosing processes: they are narrowed posteriorly and do not enclose the large rounded anterior palatal foramina, making a V-shaped junction with the maxillae. The palation is square, with a post-palatal spicule. The mesopterygoid fossa is wide, with a blade-like, projecting vomer. The pterygoids are long and flaring, partially concealing large lateral apertures, although the sphenoidal bridge is narrow. There is a shallow sphenoidal depression. The cochleae are large, their width equal to two times or a little more their distance apart, with a rather narrow basioccipital. The upper incisors lack the outer lobe, and although convergent their tips are widely separated. The upper canines have weak anterior and posterior cusps. The anterior upper premolar (pm^2) is of moderate size, slightly extruded and compressed between the canine and the second upper premolar (pm^4). The posterior ridge of the third upper molar is one half or slightly less the length of the anterior ridge. The crown area of the outer lower incisors is slightly greater than that of the inner lower incisors and the anterior lower premolar (pm_2) is equal approximately to one half the length and height of the second lower premolar (pm_4).

Hayman (1947 : 73) pointed out that *H. jonesi* stood apart from any of the groups defined and keyed by Tate (1941), noting that while in size, the form of the ears and in the mastoid width exceeding the zygomatic width it approached the *bicolor* group of species as understood by Tate, in other features such as the well-developed single supplementary leaflet and the absence of a frontal sac it differed widely from this and the other groups of the genus. Later, Aellen (1954 : 480) keyed and listed *H. jonesi* as the sole species of a *jonesi* group. However, there seems little doubt that *H. jonesi* should be allocated to the group of species typified by *H. bicolor* and its allies. As in these species, the ears have a distinct internal fold and are haired for one third of their length. The skull has the elongate outline typical of *H. bicolor* and its associated species, with a similarly broad braincase. The nearest ally to *H. jonesi* appears to be *H. ridleyi*, a Malaysian species exhibiting similar specialization of the noseleaf, although as might be expected from the wide geographical separation of the two species, there are very considerable differences between them. Both have large, sub-triangular ears with a well-defined internal fold : their noseleaves are wide, covering the muzzle almost entirely : in each the internarial septum is expanded to form a disc-like structure and circumnarial pockets have been developed while both have a high posterior leaf, its lower half deeply pocketed and its upper half smooth. *Hipposideros jonesi* differs markedly from *H. ridleyi* in the possession of a well-developed lateral supplementary leaflet which in *H. ridleyi* is merely incipient : the internarial disc in *H. jonesi* is larger and the posterior leaf more developed, with its upper edge triangular in outline and not rounded as in *H. ridleyi*. Cranially, the two species are closely similar and have skulls essentially resembling those of *H. bicolor* and its immediate allies : *H. jonesi* has a smaller, more slender skull than *H. ridleyi* with a square and not U-shaped palation and larger cochleae, with narrowed basioccipital and sphenoidal bridge. Their dentition differs principally in that the upper incisors of *H. jonesi* are placed at the outer margins of the premaxillae and although convergent have their tips separated: those of *H. ridleyi* are more medially sited and have their tips strongly convergent and almost touching. *Hipposideros jonesi* is the most specialized species of the more primitive *bicolor* section of the *bicolor* group, retaining the more or less rounded ears, elongate rostrum and narrowed zygomata of the *bicolor* type and yet with a greatly specialized noseleaf associated with some specialization of the auditory region of the skull. Together with the similar but less specialized species *H. ridleyi* it constitutes an offshoot of the *bicolor* type leading apparently to no further specialization. Its differences from the Malaysian *H. ridleyi* are of a considerable order of magnitude and indicate remote separation of the parental stems.

DISTRIBUTION: West Africa: Sierra Leone; Guinea (for notes on specimens from Guinea see Eisentraut & Knorr (1957 : 333)).

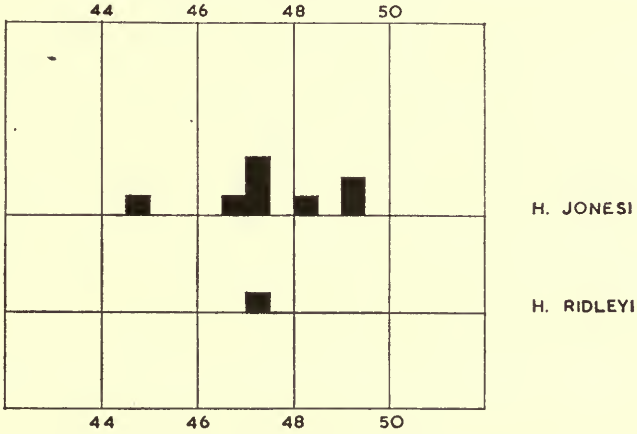


FIG. 10. Length of forearm in *Hipposideros jonesi* and *H. ridleyi*

Hipposideros dyacorum Thomas

Hipposideros dyacorum Thomas, 1902 : 271. Mount Mulu, Baram, Sarawak, Borneo.

The ears are of moderate size, broad at the base, sub-triangular, their anterior margins convex, their posterior margins with a slight concavity just behind the tip but otherwise convex. There is a well-defined internal fold at the antitragal lobe and the ears are sparsely haired for about one half of their length. The noseleaf is small, narrow and simple, and lacks lateral supplementary leaflets. It is very like the noseleaf of *H. bicolor*, with the internarial septum slightly inflated, triangular, broad at its base, narrowed between the nostrils and with the narial margins of the anterior leaf slightly expanded but not concealing the nostrils. The intermediate part of the leaf is cushion-like, with a low, slightly inflated median eminence. The posterior leaf is thin, its upper edge semicircular, and is supported by a well-defined median septum and two less prominent lateral septa. There is a small frontal sac in the female type specimen.

The skull is short and the braincase strongly inflated with a low sagittal crest. The interorbital region is constricted and the supraorbital ridges, although low, are sharply defined and prominent. There is a shallow frontal depression and the rostrum is slightly broadened, with moderately inflated rostral eminences. The zygomata are slender with a moderate jugal projection, and the anteorbital foramen is elongate, closed by a very slender bar. The premaxillae are entirely fused, their junction with the maxillae shallowly V-shaped, the maxillae with an abrupt emargination at the apex of the V. The enclosing processes of the premaxillae are delicate and hook-shaped, but do not enclose the rounded anterior palatal foramina. The palation is U-shaped, with an abrupt median emargination. The vomer does not project into the mesopterygoid fossa, which is not greatly widened. The pterygoids are long, the pterygoid wings flaring, together with the slightly constricted sphenoidal bridge partially concealing elongate lateral apertures. There is a shallow sphenoidal depression. The width of the cochleae is equal to their distance apart. The upper incisors are very weakly bilobed, and the upper canines have weak anterior and posterior cusps. The anterior upper premolar (pm^2) is minute, extruded, with the canine and the second upper premolar (pm^4) in contact. The posterior ridge of the third upper molar is obsolete. The crown area of the outer lower incisors is very slightly greater than that of the inner lower incisors. The anterior lower premolar (pm_2) is much reduced, to one quarter the length and height of the second lower premolar (pm_4). Measurements of specimens of *H. dyacorum* from southwestern Borneo are given by Lyon (1911 : 129, 130) while a description, with measurements, of a series from North Borneo is provided by Davis (1962 : 39).

Hipposideros dyacorum forms a link between *H. bicolor* and *H. galeritus*, and although independently slightly specialized in some respects displays some characters indicative of the aggregations of species to which they belong. The ears and noseleaf of *H. dyacorum* correspond closely to those of *H. bicolor* and its allies, while its skull is shortened like that of *H. galeritus* and its associated species, and has the long pterygoids common to both aggregations of species. The dentition of *H. dyacorum* is more advanced than that of *H. bicolor* and its allies and in the reduction of the premolars tends towards *H. galeritus*.

DISTRIBUTION : Borneo.

Hipposideros sabanus Thomas

Hipposideros sabanus Thomas, 1898 : 243. Lawas, North Borneo.

The ears are large and broad, rounded and not acutely pointed, their posterior margins evenly convex. They are thickened at the antitragal lobe but lack a definite internal fold, and are haired for the basal third of their length. The noseleaf is small and comparatively simple, lacking lateral supplementary leaflets. The anterior leaf is narrow, with a well-defined median emargination. The internarial septum is swollen and bulbous, especially posteriorly, but does not conceal the narial apertures, which are flanked by small narial lappets. The intermediate part of the leaf is cushion-like but not greatly inflated. The posterior leaf is high, without supporting septa and has a semicircular upper edge. It is specialized by the development from its posterior face of a transverse supplementary structure, with a slightly serrate upper edge below that of the posterior leaf. There is a small frontal sac in the female type specimen.

The skull is small, with a broad braincase and low sagittal crest. The interorbital region is moderately constricted while the supraorbital ridges are not sharply defined and are very weak. There is no frontal depression, the rostrum in profile exhibiting a slight convexity. The rostrum is short and not broadened, the rostral eminences only slightly inflated. The zygomata are slender with a high jugal process, their combined width greater than the mastoid width. The anteorbital foramen is elongate, closed by a very slender bar. The premaxillae are short and broad, their junction with the maxillae V-shaped, while the anterior palatal foramina are rounded and enclosed within the premaxillae by a narrow bar. The palation is only slightly rounded, almost square, without a median emargination. The mesopterygoid fossa is wide, with a slightly projecting vomer, while the pterygoids are short and the sphenoidal bridge narrow, exposing large rounded lateral apertures. There is a shallow sphenoidal depression and the cochleae in width slightly exceed their distance apart. The upper incisors are not bilobed, the outer lobe obsolete, while the upper canines have a weak anterior cusp and a trace of the posterior cusp. The anterior upper premolar (pm^2) is obsolete, the second upper premolar (pm^4) with a low anterior cusp in contact with the canine. The posterior ridge of the third upper molar is reduced to one third the length of the anterior ridge. The crown area of the outer lower incisors is very slightly greater than that of the inner lower incisors, while the anterior lower premolar (pm_2) is much reduced, one quarter the length and height of the second lower premolar (pm_4) and is slightly extruded from the toothrow.

The collections of the British Museum (Natural History) contain a specimen from Sumatra (B.M. 27.5.9.3) which hitherto has been referred to *H. doriae* (Peters). However, its ears agree exactly with those of *H. sabanus*, and although the noseleaf has been partially destroyed, sufficient remains intact to show that the posterior leaf lacks supporting septa and has the low transverse serrated supplementary structure typical of *H. sabanus* developed from its posterior face. Cranially, this specimen agrees very closely with *H. sabanus* but has the sphenoidal depression a little more sharply defined and the upper incisors weakly bilobed, the outer lobe obsolescent. In view of these considerations it is referred to *H. sabanus*, which Chasen (1940 : 481) had already recorded from Sumatra.

I am unable to agree with Tate (1941 : 366, 383, 388) that *H. dyacorum* and *H. sabanus* are closely related or even allied. At most they appear to share a common origin among the more primitive bats of the *bicolor* subgroup to which they both display affinity, but otherwise they appear to represent two differing and widely divergent lines of development. Although *H. dyacorum* has more or less triangular ears with a slight posterior concavity, its ears nevertheless have a well-defined internal fold and its noseleaf is simple, lacking lateral supplementary leaflets.

Hipposideros sabanus has the broad, rounded ears characteristic of the *bicolor* subgroup, with convex posterior edges but without an evident internal fold. Its noseleaf, although rather small, without lateral supplementary leaflets and basically of the *bicolor* type, is more specialized, with the posterior leaf lacking supporting septa and with a transverse supplementary structure on its posterior face. The two species differ sharply in their cranial characters. *Hipposideros dyacorum* has a longer skull than *H. sabanus*, and has a wider rostrum with the rostral eminences more inflated. The palate in *H. dyacorum* is very much longer and the palation U-shaped and not square : its pterygoids are long and the sphenoidal bridge is wide, in contrast to *H. sabanus*, which has short pterygoids and a narrow sphenoidal bridge. The anterior lacerated foramina of *H. dyacorum* are elongate and narrow, while those of *H. sabanus* are rounded and wide. These differences in cranial architecture indicate considerable separation, and the two species do not appear to be closely related.

Hipposideros dyacorum appears to be more closely related to *H. bicolor* and its immediate allies than does *H. sabanus*. Its ears retain the internal fold : its noseleaf is largely unspecialized and the skull is slightly elongate, the palate not extensively shortened. Its long pterygoids and wide sphenoidal bridge suggest relationship with *H. galeritus* and its associated species and it is clearly derived from the line connecting them to the less specialized species associated with *H. bicolor*. *Hipposideros sabanus*, although with ears of the *bicolor* type, has a more advanced noseleaf and a shorter, less elongate skull. Its much shorter palate indicates closer relationship to the *galeritus* subgroup than is evident in *H. dyacorum* : the features of its posterior leaf, which lacks supporting septa and which has a low posterior transverse structure, together with the short pterygoids and narrow sphenoidal bridge suggest that it has been derived from the stem leading to *H. caffer* and its allies.

DISTRIBUTION : Borneo ; Sumatra.

Hipposideros doriae (Peters)

Phyllorhina doriae Peters, 1871a : 326. Sarawak, Borneo.

The collections of the British Museum (Natural History) contain no specimen referable to *H. doriae* and it has not been possible to examine the type specimen, described by Peters from the collections of the Marquis J. Doria and apparently deposited in the collections of the Museo Civico di Storia Naturale at Genoa. Although Peters described only the external features of *H. doriae* there seems little doubt from his description that it belongs to that section of the genus typified by *H. bicolor* and is very similar, if not identical to *H. sabanus*. The ears lack a distinct tip and have their anterior and posterior margins equally convex for their terminal third. The noseleaf lacks supplementary lateral leaflets and the posterior leaf has a smooth anterior face, without supporting septa. There is a small but distinct frontal sac. Further notes on the type specimen were obtained by Oldfield Thomas from R. Gestro of the Museo Civico di Storia Naturale and are preserved in the archives of the British Museum (Natural History) for 1902. They have also been recorded by Thomas as a marginal note to the account of *H. doriae* (p. 146) in a copy of Dobson, 1878, Catalogue of the Chiroptera in the collection of the British Museum, now in the library of the British Museum (Natural History). The features of the type specimen noted by Gestro are that the anterior leaf has no median emargination : that the anterior upper premolar (pm^2) is absent and that the anterior lower premolar (pm_2) is small, a diagram drawn by Gestro suggesting that it is less than one half of the size of the second lower premolar (pm_4). Thomas adds in his marginal note that *H. sabanus* is probably equal to *H. doriae* : the close agreement of noseleaf and dentition suggests that *H. doriae* is related to *H. sabanus* rather than to *H. bicolor* as was suggested by Dobson (1878 : 147) and Tate (1941 : 383). The two species are clearly very similar and seem likely to be at least conspecific, in which case it should be noted that *doriae* is the prior name by many years.

Hipposideros obscurus (Peters)

Phyllorhina obscura Peters, 1861 : 709. Paracali, Luzon, Philippine Islands.

The following notes are based on a small series (B.M. 77.10.6.14–18) in the collections of the British Museum (Natural History), from Dinagat Island, Philippine Islands, consisting of an adult male and female, together with three young males. The ears are sharply triangular, broad at the base, their anterior margins markedly convex and their posterior margins with a concavity just behind the acute point. There is no internal fold but the ear membrane is thickened at the antitragal lobe and there is a small antitragal projection. The ears are haired for one half of their length. The noseleaf is of moderate size and does not entirely cover the muzzle : it lacks lateral supplementary leaflets but has a distinct raised glandular ridge directly beneath the edge of the anterior leaf, extending laterally under the margins of the anterior leaf and anteriorly beneath this leaf to the median line. The anterior leaf in the adult male has a small but distinct median emargination which in the adult female is very small : it is present but very small in two of the young male specimens and absent in the third. The internarial septum is not inflated and is broadly triangular, narrow between the nostrils, which lie at the base of a deep depression : the narial lappets are moderately developed and the narial margins of the anterior leaf are slightly expanded. The intermediate part of the leaf is cushion-like, slightly inflated, with a low median ridge or eminence. The posterior leaf is high, its upper edge semicircular and lacks supporting septa, with a low transverse ridge on its posterior face. There is a well-developed frontal sac in the male, represented by a depression in the female specimen.

The skull is short and comparatively broad, with a broad, inflated braincase, low sagittal crest and a moderately constricted interorbital region. There is no frontal depression and the rostrum is broad and rounded, with slightly inflated rostral eminences. The zygomata are slender, their combined width a little greater than the mastoid width. The anteorbital foramen is large and elongate, closed by a narrow bar. The junction of the premaxillae with the maxillae is shallowly V-shaped and the palate is short : the palation is U-shaped with a small post-palatal spicule.

The mesopterygoid fossa is wide, the vomer not projecting and the pterygoids long, together with the moderate sphenoidal bridge partially concealing wide lateral apertures. There is a small sphenoidal depression and the width of the cochleae is equal to their distance apart. The anterior upper premolar (pm^2) is small and is extruded into the angle between the canine and the second upper premolar (pm^4), which however are not in contact, while the posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is slightly greater than that of the inner pair. The anterior lower premolar (pm_2) is three quarters the length and height of the second lower premolar (pm_4).

Hipposideros obscurus is the last species of the *bicolor* type and like *H. dyacorum*, apparently links the more primitive of these to *galeritus* and its allies, although it has no apparent close connection with *H. dyacorum* and in some respects inclines towards *H. sabanus*. Its ears are very like those of *H. dyacorum* but lack the internal fold while its noseleaf, although of *bicolor* type, has deeply depressed nostrils suggestive of *H. pygmaeus* or *H. coxi*, and a posterior leaf lacking septa and with a posterior transverse structure reminiscent of *H. sabanus*. The short, broad skull has the long pterygoids characteristic of *H. galeritus* and its associates as distinct from *H. caffer* and its allies but the dentition, retaining the anterior upper premolar, is less advanced than in *H. dyacorum* and *H. sabanus*.

DISTRIBUTION : Philippine Islands : Luzon ; Dinagat ; Mindanao (Sanborn (1952 : 104)).

Hipposideros marisae Aellen

Hipposideros marisae Aellen, 1954 : 474, fig. 1. White Panther Rock, Duékoué, Ivory Coast.

No example of *H. marisae* has been examined, and the following notes have been compiled from the original description. The ears are large, broad and bluntly pointed, with a concavity behind the tip. There is no antitragal fold. The noseleaf is small with one very small lateral supplementary leaflet. The anterior leaf has apparently no median emargination and the internarial septum is inflated, slightly disc-like between the nostrils. The intermediate part of the leaf is slightly inflated while the posterior leaf is high, its upper edge semicircular, and is supported by three septa enclosing deep pockets. A frontal sac is present in the male type specimen.

The skull is said to be in general similar to that of *H. bicolor* and *H. curtus*, with a weak sagittal crest, narrow rostrum, comparatively wide zygomata, their combined width greater than the mastoid width, and small bullae. The dentition is apparently similar to that of *H. curtus* : the upper incisors lack the outer lobe and the anterior upper premolar (pm^2) is small and slightly extruded while the anterior lower premolar (pm_2) is one half the height of the second lower premolar (pm_4).

Aellen (1954 : 474 et seq.) has considered the taxonomic status of *H. marisae* and its relative *H. curtus* in some detail, and concluded that neither are closely related to *H. caffer* and its immediate allies but to the *bicolor* group (the *bicolor* subgroup as here understood). Aellen further proposed that *H. marisae* and *H. curtus* should be considered to represent a group within *Hipposideros*, the *curtus* group, characterized by large emarginated ears lacking an internal fold, one or two lateral supplementary leaflets, swollen claviform internarial septum, the presence of a frontal sac in males, sometimes absent in females, the fourth metacarpal longer than the third and fifth and by a small, slightly extruded anterior upper premolar (pm^2). However, there seems no justification for this action. *Hipposideros curtus*, with ears and noseleaf similar to those of the *bicolor* subgroup yet with two lateral supplementary leaflets and skull tending towards the *galeritus* subgroup, particularly towards *H. caffer*, is clearly derived from the *bicolor-caffer* stem. Similarly, another such derivative, *H. fuliginosus*, which Aellen places in a *caffer* group, has ears and noseleaf closely similar to those of *H. caffer*, yet has a skull exhibiting a number of the features of the *bicolor* subgroup. From the original description, *H. marisae* presents yet a further combination of characters, having slightly specialized ears lacking an internal fold but otherwise like those of the *bicolor* subgroup and in the possession of a simple noseleaf similar to that of *H. bicolor*, with one small, rudimentary lateral supplementary leaflet. Its skull appears to be similar to the skulls of the members of the *bicolor* subgroup, rather elongate and narrow, with the zygomatic width only barely exceeding the mastoid width. It too represents the *bicolor-caffer* stem, and is a less advanced species than either *H. curtus* or *H. fuliginosus*.

Hipposideros marisae, *H. curtus* and *H. fuliginosus* form connecting links between *H. bicolor* and its associated species and the more specialized *H. caffer*. As is not unusual in the genus, specialization of the various species has reached different levels : *H. marisae* and *H. curtus* have ears and noseleaves rather of the pattern of *H. bicolor*, modified by the presence of one lateral supplementary leaflet in *H. marisae* and the presence of two such leaflets in *H. curtus*, while *H. marisae* has a skull of the *bicolor* type and *H. curtus* a skull tending towards *H. caffer*. *Hipposideros fuliginosus* has *caffer*-like ears and noseleaf associated with a skull similar to that of the members of the *bicolor* subgroup. The characters of its ears and noseleaf ally it more closely to *H. caffer* than to *H. marisae* and *H. curtus* and it is less closely related to these species than they are to each other. Both are characterized by a swollen, claviform internarial septum which tends to form a disc-like structure between the nostrils, a specialization found in far more greatly developed form in *H. ridleyi* and *H. jonesi*, two species forming a development of *H. bicolor* and its allies. For this reason, *H. marisae* and *H. curtus* are considered to form an independent offshoot of the *bicolor-caffer* stem. There seems little point in constructing groups for intermediate species, based largely on the characters that they share in common with the species they link together, and the *curtus* group of Aellen (1954 : 479) in the present work is considered to form a part of the *bicolor* group as here understood.

Hipposideros pygmaeus (Waterhouse)

Rhinolophus pygmaeus Waterhouse, 1843 : 67. Philippine Islands.

The type specimen is the only available example of *H. pygmaeus*. It is a very small bat with the ears sub-triangular, very broad at the base, pointed, with the upper portion of their anterior margins very slightly concave and their posterior margins concave behind the tip. The ears are slightly thickened at the antitragal lobe and are haired for one half of their length. The noseleaf is large, entirely covering the muzzle, and has two lateral supplementary leaflets, the anterior leaflet extending from the base of the intermediate part of the leaf forward beneath the anterior leaf to the median line but with a median emargination, the posterior leaflet well developed and extending slightly anteriorly. The internarial septum is very small and reduced, insignificant between the nostrils : the narial lappets are greatly developed, especially laterally, and rise above the level of the horseshoe. They are elongated and almost completely encircle the nostrils, which lie at the base of the small pockets so formed. The intermediate part of the leaf is well inflated but lacks eminences. The posterior leaf is high, thin, its upper edge semicircular, and is supported by three well-defined septa which enclose four small but moderately deep pockets. There is no frontal sac in the female type specimen : according to Tate (1941 : 369) it is present in males.

A small anterior portion of the skull is all that remains. The sagittal crest, represented by a remnant, is evidently low and the interorbital region is constricted, but not sharply so, with no evident supraorbital ridges. There is no frontal depression. The rostrum is slightly shortened, high and rounded, the rostral eminences well inflated with a slight median depression between them. The anteorbital foramen is large and rounded, closed by a very narrow bar. The upper incisors are weakly bilobed, the outer lobe obsolescent. The upper canines have a moderate anterior cusp and a stronger posterior cusp extending for about one third of the length of the tooth. The anterior upper premolar (pm^2) is small but is barely out of alignment in the toothrow, separating the canine and the second upper premolar (pm^4), which has a distinct anterior cusp. The posterior ridge of the third upper molar is one half of the length of the anterior ridge.

Tate (1941 : 367, 369, 388) considered *H. pygmaeus* to be an isolated species derived from the line leading to *H. galeritus* and its allies. This view appears to be correct, and despite its extended anterior lateral supplementary leaflets and inflated rostral eminences which suggest relationship to *H. coxi*, its affinities lie more closely with *H. galeritus* and its associated species. Although the anterior lateral supplementary leaflets in *H. pygmaeus* extend anteriorly beneath the anterior leaf to the median line as in *H. coxi*, the two species differ sharply in that the leaflets in *H. pygmaeus* are not continuous over the upper lip as in *H. coxi*, but are divided to the base by a sharp median emargination. This condition suggests *H. galeritus*, in which the leaflets, although extending forward beneath the anterior leaf, do not reach the median line. The narial part of the noseleaf in *H. pygmaeus* is slightly more specialized than that of *H. obscurus*, also a derivative of the *galeritus* stem. The posterior leaf is divided by blade-like septa as in *H. galeritus*, and its margins at the base display none of the extraordinary complexity of *H. coxi*. The skull is not excessively shortened and the dentition not greatly specialized, providing a link with the *bicolor* type of skull. Vertical inflation of the rostral eminences appears to be a correlation of increasing complexity of the narial region of the noseleaf. *Hippo-*

sideros obscurus, in which the narial apertures are situated at the base of a deep depression but are not noticeably pocketed, has slightly inflated rostral eminences. In *H. pygmaeus* the narial region is slightly more specialized : the narial lappets are elongated to form small pockets almost completely encircling the nostrils and the rostral eminences are well inflated. *Hipposideros coxi* has the narial apertures completely concealed within a pocket formed by the narial lappets and the internarial septum : correspondingly the rostral eminences are much inflated and appear as two separate raised structures. On the balance of characters, therefore, *H. pygmaeus* is associated with *H. galeritus* and its allies.

DISTRIBUTION : Philippine Islands : Luzon ; Negros (Sanborn (1952 : 104)).

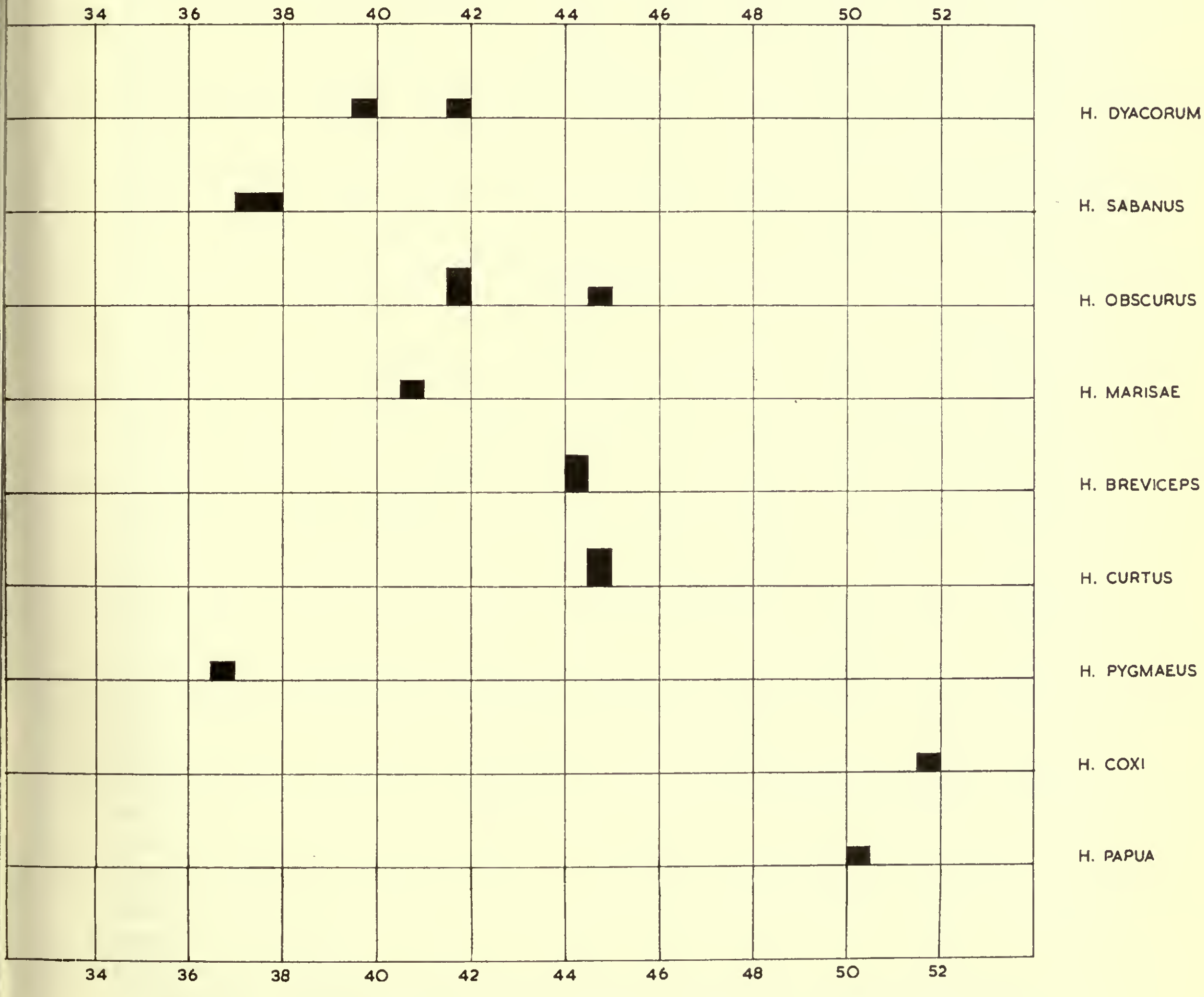


FIG. 11. Length of forearm in *Hipposideros dyacorum*, *H. sabanus*, *H. obscurus*, *H. marisae*, *H. breviceps*, *H. curtus*, *H. pygmaeus*, *H. coxi* and *H. papua*

Hipposideros galeritus

The ears are broad, triangular and acutely pointed, their anterior margins convex, their posterior margins concave behind the tip but otherwise convex, without a marked antitragal fold but thickened at the antitragal lobe, with a small antitragal projection. They are haired for three quarters of their length. The noseleaf is small and comparatively simple, with two well-developed lateral supplementary leaflets, which project beyond the lateral margins of the anterior leaf. The anterior lateral supplementary leaflet extends from the base of the posterior leaf anteriorly beneath the anterior leaf on to the upper lip but does not reach the median line. This condition is similar to that found in *H. pygmaeus*, in which the anterior leaflets on each side do in fact extend anteriorly to the median line, but are separated by a deep emargination above the centre of the upper lip. The posterior lateral supplementary leaflet is broad but is shorter than the anterior leaflet, only just extending on to the upper lip. The anterior leaf is not emarginated. The internarial septum is more or less parallel-sided and is not inflated : the narial lappets are well developed and project slightly above the level of the anterior leaf. Although lying in a depression, the nostrils are not enclosed by narial pockets. The intermediate part of the leaf is slightly inflated and cushion-like but has no swollen prominences. The posterior leaf is thin, its upper edge semicircular with no trace of lobulation, and is supported by three well-defined septa enclosing four small pockets. There is a frontal sac in males, represented in female specimens by a depression containing a tuft of hairs.

The skull is short and broad, with an inflated, almost globose braincase and a low to moderate sagittal crest. The interorbital region is constricted, with sharply defined supraorbital ridges. There is a shallow frontal depression and the rostral eminences are moderately inflated, separated by a shallow groove. The zygomata are slender, with a low to moderate jugal projection, the zygomatic width exceeding the mastoid width. The postorbital processes are incipient, giving the rostrum from above a slightly pentagonal aspect. The anteorbital foramen is elongate and closed by a narrow bar. The premaxillae are fused for their entire length, their junction with the maxillae shallowly V-shaped. Their anterior enclosing processes are slender and do not entirely enclose the more or less oval anterior palatal foramina. The palate is short and broad, the palation U-shaped with usually a small median post-palatal spicule. The mesopterygoid fossa is wide, the vomer not projecting or projecting only slightly, the pterygoids elongated, with the wide sphenoidal bridge partially concealing elongate lateral apertures. There is a well-defined sphenoidal depression, while the width of the cochleae is a little greater than their distance apart. The upper incisors are not bilobed or are only very weakly bilobed, with only a trace of the external lobe. The upper canines have a moderate anterior cusp and a well developed posterior cusp, both low. The anterior upper premolar (pm^2) is usually much reduced, minute, extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is reduced to one third of the length of the anterior ridge. The crown area of the outer lower incisors is about the same or very slightly greater than that of the inner pair. The anterior lower premolar (pm_2) is usually reduced to one half or less of the length and height of the second lower premolar (pm_4).

DISTRIBUTION : India ; Malay Peninsula east to Solomon Islands and New Hebrides ; northern Australia.

Hipposideros galeritus galeritus Cantor

Hipposideros galeritus Cantor, 1846 : 183. Penang.

Tate (1941 : 367) has thrown considerable doubt on the authenticity of the skull of the type specimen of *Hipposideros galeritus* Cantor and has suggested that the skin and skull may be mismatched. The type specimen is now B.M. 79.11.21.85 in the collections of the British Museum (Natural History), a skin and skull, labelled as a male. In the register of the mammal collections in the British Museum (Natural History) for 1879, the specimen is listed as a skin only, with no mention of a skull. The skin is preserved in the dry state and fortunately is in good condition. The ears are broad at the base, triangular and sharply pointed, their posterior margins with a concavity just behind the tip. The noseleaf has two lateral supplementary leaflets and the posterior leaf is thin, supported by three septa. The skull associated with this skin is small, rather elongate, with a low sagittal crest, constricted interorbital region, no supraorbital ridges and moderately inflated rostral eminences. The zygomata are slender, with a well-developed superior projection, the zygomatic width (by extrapolation) less than the mastoid width. The anteorbital foramen is slightly elongate, closed by a narrow bar. The junction of the premaxillae with the maxillae is acutely V-shaped. The palation is U-shaped, with the vomer projecting very slightly into the mesopterygoid fossa. The sphenoidal bridge is moderate, not concealing the lateral apertures. There is a shallow sphenoidal depression. The upper incisors are weakly bilobed and the upper canines are slender, with a low posterior cusp. The anterior upper premolar (pm^2) is minute, extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact. The posterior ridge of the third upper molar is one half the length of the anterior ridge. The crown area of the outer lower incisors is slightly greater than that of the inner pair and the anterior lower premolar (pm_2) is two thirds the length and one half the height of the second lower premolar (pm_4). It is clearly the skull of a member of the *bicolor* subgroup and agrees closely with *H. ater*. It is therefore necessary to adopt the suggestion by Tate that *Hipposideros galeritus* Cantor be restricted to the skin of the type specimen, disregarding the skull hitherto associated with that skin.

The characters of *H. g. galeritus* are much as in the species diagnosis. The upper incisors are not bilobed, the outer lobe being obsolete. The anterior upper premolar (pm^2) is very small, extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact. The anterior lower premolar (pm_2) is one third to one half the length and height of the second lower premolar (pm_4). Davis (1961 : 90) gives a description, with measurements, of a series of *H. g. galeritus* from the Federation of Malaya.

DISTRIBUTION : Malay Peninsula ; Riau Archipelago ; Banka Island ; South Natuna Islands.

Hipposideros galeritus brachyotus (Dobson)

Phyllorhina brachyota Dobson, 1874b : 237. Central India.

The characters of this subspecies are largely those of the nominate subspecies, but the post-palatal spicule is usually very small or absent, and the dentition is less advanced. The anterior upper premolar (pm^2), although small, is not always completely extruded from the toothrow but is compressed tightly between the outer margins of the canine and the second upper premolar (pm^4), while in some specimens it is extruded from the toothrow with the canine and the second upper premolar in contact. The posterior ridge of the third upper molar is one half the length of the anterior ridge. The anterior lower premolar (pm_2) is less reduced than in *H. g. galeritus*, and is nearly as long as the second lower premolar (pm_4) and two thirds its height. Brosset (1962 : 618) has studied the biology of *H. galeritus* in India, and gives measurements and notes on its colour variation.

DISTRIBUTION : Ceylon ; India : Mysore ; Bombay ; Bengal.

Hipposideros galeritus schneideri Thomas

Hipposideros schneidersi Thomas (misprint), 1904b : 722. Upper Langkat, Sumatra.

The posterior leaf is supported by a prominent median septum, the lateral septa not greatly developed and represented by low ridges. The post palatal spicule is absent. The upper canines have a low anterior cusp, their posterior cusp insignificant or low. The anterior upper premolar (pm^2) is minute or lacking (it is absent in one side of the jaw of the type specimen, vestigial in the other side) the canine and the second upper premolar (pm^4) in contact. The anterior lower premolar (pm_2) is much reduced and is one third to one half the length and height of the second lower premolar (pm_4). Tate (1941 : 367) suggests that *H. g. schneideri* is a derived species of *H. galeritus*. There seems no reason, however, to separate it from this species with which it shares a majority of characters, differing principally in the greater reduction of the anterior premolars.

DISTRIBUTION : Sumatra ; Engano Island ; Sipora Island ; Mentawi Islands : North Pagi.

Hipposideros galeritus labuanensis (Tomes)

Phyllorrhina labuanensis Tomes, 1859a : 537. Labuan Island.
Hipposideros insolens Lyon, 1911 : 129. Upper Pasir River, southeastern Borneo.

This subspecies is very similar to *H. g. galeritus*. The post-palatal spicule may be present or absent and there is a well-defined sphenoidal depression. The upper incisors are not bilobed or only slightly so, and the upper canines have well defined anterior and posterior cusps. The anterior upper premolar (pm^2) is small, extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is one third to one half the length of the anterior ridge. The anterior lower premolar (pm_2) is reduced to

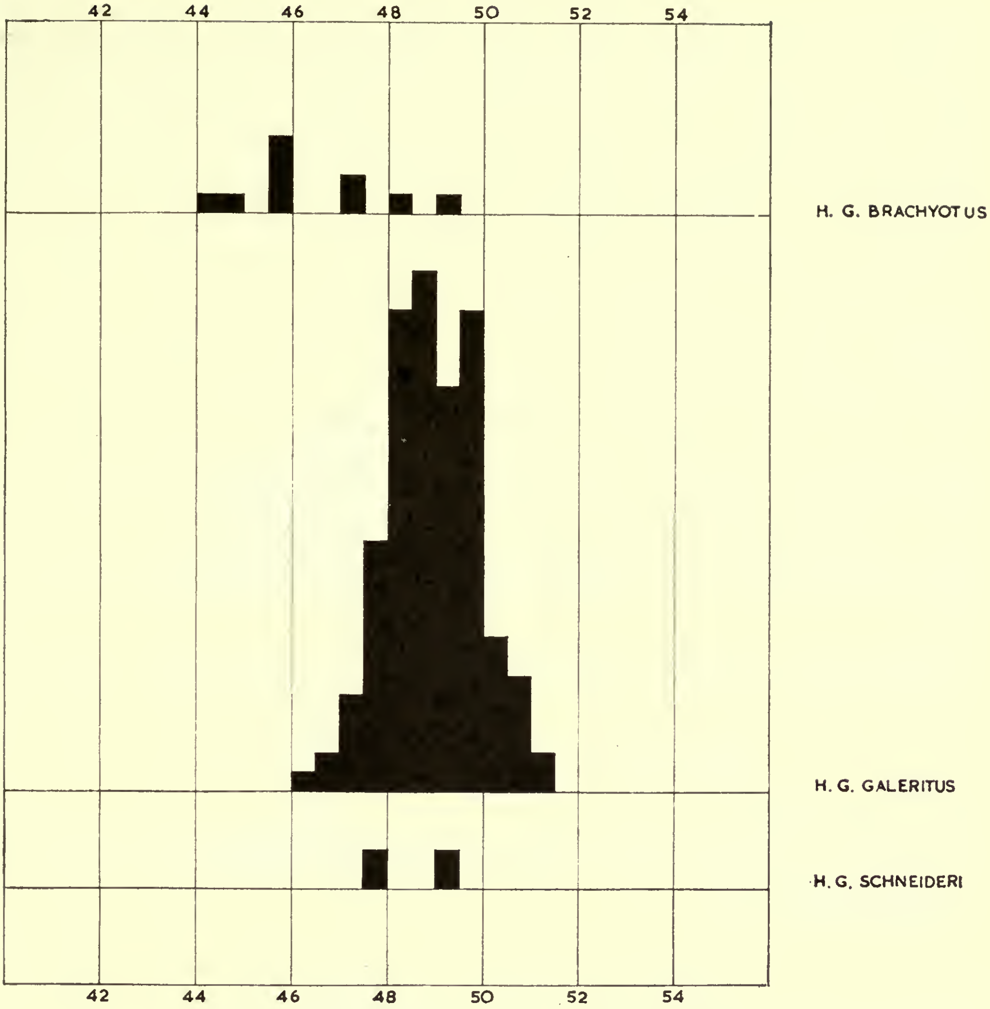


FIG. 12. Length of forearm in *Hipposideros galeritus*

one half or a little less the length and height of the second lower premolar (pm_4) to two thirds its length and height. Davis (1962 : 39) provides a description, with measurements, of a series of *H. g. labuanensis* from North Borneo.

Lyon originally described *H. insolens* as a species distinct from *H. galeritus*, recording both from the same localities in Borneo. According to Lyon the distinguishing characters of *H. insolens* were its longer forearm and tibia when compared with *H. galeritus*. Chasen (1940 : 46) listed *H. insolens* as a subspecies of *H. longicauda*, here considered to be a subspecies of *H. galeritus*. Tate (1941 : 368) retained *H. insolens* as an apparently distinct species and from an examination of the original series described by Lyon stated that in comparison with *H. g. labuanensis* the jugal prominence of the zygoma in *H. insolens* rose more abruptly, the anteorbital foramen was almost pore-like and not elongate as in *H. g. labuanensis* while the palate was a little longer (extending a little behind the second upper molar) and lacked a spine. He also noted that the toothrow was shorter, with the W-pattern of the third upper molar less reduced and that the anterior lower premolar (pm_2) was more elongate than wide. No topotypical specimens of *H. insolens* are available but the collections of the British Museum (Natural History) contain an adequate series of *Hipposideros galeritus* from Borneo and this series suggests that *H. insolens* as understood by Lyon and Tate may well refer to large individuals of *H. g. labuanensis*. The jugal prominence in a long series of *H. g. labuanensis*, although usually moderate in its development is sometimes found to be not greatly developed, rising only gently from the zygoma while the anteorbital foramen, usually elongate, is on occasion rounded and more pore-like. The rear of the palate varies from a line joining the posterior faces of the second upper molars (m^{2-2}) to a line joining the centres of the third upper molars (m^{3-3}), while the postpalatal spicule is sometimes absent or incipient. The length of the posterior ridge of the third upper molar varies from one third to one half the length of the anterior ridge, while the anterior lower premolar (pm_2) varies from less than one half the length and height of the second lower premolar (pm_4) to two thirds its length and height.

DISTRIBUTION : Borneo ; Labuan Island ; Philippine Islands : Mindanao (Sanborn (1952 : 104) as *H. g. galeritus* : see also Laurie & Hill (1954 : 55)).

Hipposideros galeritus longicauda (Peters)

Phyllorhina longicauda Peters, 1861 : 708. Java.

There are no specimens of this subspecies in the collections of the British Museum (Natural History). Sody (1930 : 270) describes four specimens in some detail.

DISTRIBUTION : Java.

Hipposideros galeritus celebensis Sody

Hipposideros celebensis Sody, 1936 : 47. Mampoe Cave, 20 kilometres north of Watoe Pone, south Celebes.

There are no specimens of this subspecies in the collections of the British Museum (Natural History). A detailed description (as *H. g. galeritus*) is given by Sody (1930 : 268) of specimens from Celebes subsequently described by the same author as *H. celebensis*.

DISTRIBUTION : Celebes.

Hipposideros galeritus batchianus Matschie

Hipposideros batchianus Matschie, 1901 : 273. Batchian Island, Molucca Islands.

There is no example of this subspecies in the collections of the British Museum (Natural History).

Hipposideros galeritus cervinus (Gould)

Rhinolophus cervinus Gould, 1863 : pl. 34, letterpress. " Caves on Albany Island " (label on skin of type specimen). Cape York, northern Queensland, Australia.

The characters of this subspecies are largely those of the nominate subspecies, the anterior upper premolar (pm^2) reduced, extruded from the toothrow, the canine

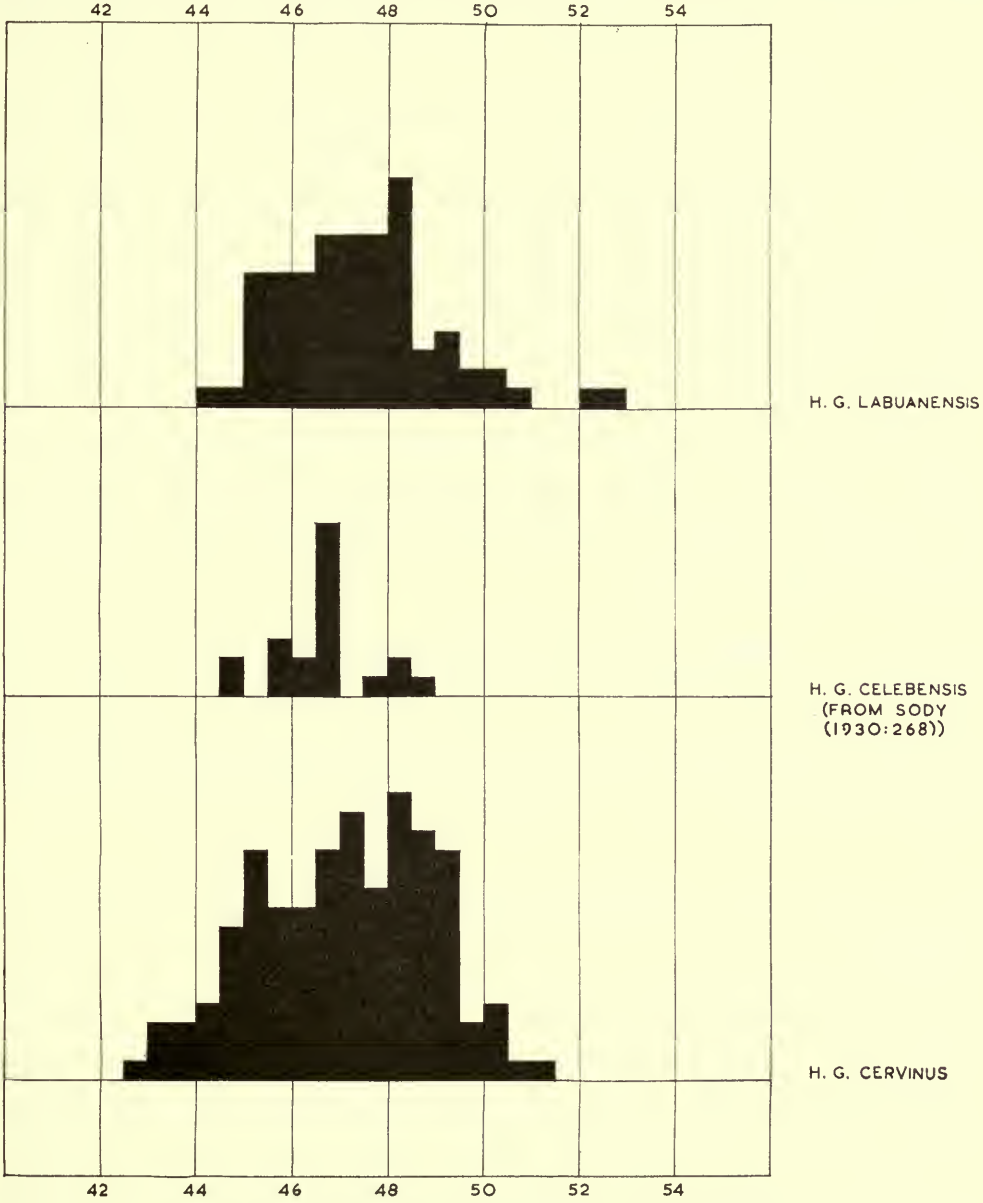


FIG. 13. Length of forearm in *Hipposideros galeritus*

and the second upper premolar (pm^4) in contact or nearly so and the anterior lower premolar (pm_2) usually one half or less the length and height of the second lower premolar (pm_4). Specimens from the Aru Islands have the anterior upper premolar (pm^2) much reduced, sometimes minute while in those from the Kei Islands this tooth is minute, almost invisible. Specimens from both groups of islands have the anterior lower premolar (pm_2) usually less than one half the length and height of the second lower premolar (pm_4). Those from Japen Island have a small but clearly visible anterior upper premolar (pm^2) and have the anterior lower premolar (pm_2) one half the length and height of the second lower premolar (pm_4). In specimens from New Guinea the anterior upper premolar (pm^2) is rather larger and more prominent while the anterior lower premolar (pm_2) is one half the length and height or slightly more of the second lower premolar (pm_4). Examples from New Ireland, the Solomon Islands, the New Hebrides and Cape York exactly resemble those from New Guinea but a single specimen from Kiriwina Island has the anterior lower premolar (pm_2) larger, equal nearly to two thirds the length and height of the second lower premolar (pm_4). There is some size variation over the range, specimens from the Aru and Kei Islands, Japen Island, Cape York and the Solomon Islands having the forearm averaging slightly shorter than those from New Guinea and the New Hebrides.

DISTRIBUTION : New Guinea ; Waigeo Island ; Japen (=Jobi) Island ; Kei Islands ; Aru Islands ; northern Australia ; Bismarck Archipelago : New Ireland ; Trobriand Islands : Kiriwina ; Solomon Islands : Bougainville ; Guadalcanar ; Fauro ; Russell ; Rennell ; New Hebrides : Espiritu Santu ; Efate ; Santa Cruz Islands : Fenvaloa ; Vanikoro.

Hipposideros crumeniferus (Lesueur & Petit)

Rhinolophus crumeniferus Lesueur & Petit, 1807 : pl. 35. Timor Island.

The status of this early name has already been discussed. Despite a careful search by the authorities of the Muséum National d'Histoire Naturelle in Paris, no trace can be found of the type specimen.

Hipposideros breviceps Tate

Hipposideros breviceps Tate, 1941 : 358. North Pagi Island, Mentawei Islands, off west coast of Sumatra.

Through the courtesy of the authorities of the American Museum of Natural History, New York, I have been able to examine two of the paratypes of *H. breviceps* Tate. The ears are broad, triangular, their anterior margins convex and their posterior margins with a concavity behind the acute point but otherwise convex. No definite internal fold can be discerned in the dry skins, but the membrane of the ears is thickened at the antitragal lobe. The ears are haired for one half or slightly more of their length. The noseleaf is small, with two lateral supplementary leaflets projecting beyond the margins of the anterior leaf. The anterior lateral supplementary leaflet extends from the base of the intermediate part of the leaf anteriorly beneath the anterior leaf on to the upper lip, but does not reach the median line. The posterior leaflet does not extend forward in the same manner but terminates anteriorly at a point just on the upper lip. The anterior leaf has no median emargination, and the internarial septum is undeveloped. The narial lappets are well developed and project above the level of the anterior leaf. The nostrils lie in deep depressions but are not pocketed, while the intermediate part of the leaf is slightly inflated and cushion-like. The posterior leaf is high, its upper edge semicircular, and is supported by the median septum and two lateral septa.

The skull is very short and broad, with an inflated, broadened braincase and low sagittal crest. The interorbital region is moderately constricted and the supraorbital ridges are poorly defined. There is a shallow frontal depression. The rostrum is rounded and not markedly pentagonal in outline, with the rostral eminences much inflated and individually swollen, separated by a groove. The zygomata are slender, with a high, well developed jugal projection, the zygomatic width exceeding the mastoid width. The anteorbital foramen is elongate, closed by a narrow bar. The premaxillae are short and do not project beyond the canines, making a shallowly V-shaped junction with the maxillae. The palate is short, the palation shallowly U-shaped, level with a line joining the posterior faces of the third upper molars (m^{3-3}), without a post-palatal spicule. The mesopterygoid fossa is wide, the vomer not projecting, and the expanded pterygoids are long, together with the wide sphenoidal bridge almost concealing elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are a little wider than their distance apart. The upper incisors are weakly bilobed, the outer lobe obsolescent and are strongly convergent, their tips almost touching. The upper canines have a small posterior cusp. The anterior upper premolar (pm^2) is minute and completely extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is one third the length of the anterior ridge. The crown area of the outer lower incisors is very slightly greater than the crown area of the inner lower incisors, while the anterior lower premolar (pm_2) is very small, one quarter or little more the length and height of the second lower premolar (pm_4).

Externally, *H. breviceps* is very similar to *H. galeritus*, but has the ears slightly less extensively haired. The skull closely resembles that of *H. galeritus* but is relatively shorter, with more inflated rostral eminences. In the shortening of the skull it tends towards *H. dyacorum* and this feature, together with the reduction of the anterior premolars, no doubt led Tate (1941 : 358) to consider *H. breviceps* as a half-way stage between an *insolens*-like form and *dyacorum*. However, there appears to be no close relation between *H. breviceps* and *H. dyacorum*. The ears of *H. dyacorum* have a well-defined internal fold, absent in *H. breviceps*, while the noseleaves of the two species differ sharply in the absence of lateral supplementary leaflets in *H. dyacorum* and the presence of two well-developed leaflets in *H. breviceps*. The skull of *H. breviceps*, although similar in outline to that of *H. dyacorum*, is less shortened, and has a much less constricted interorbital region.

There is a shallow frontal depression, absent in *H. dyacorum*, and there are no marked supraorbital ridges like the prominent, sharply defined ridges of that species. *Hipposideros breviceps* has the palate less shortened than *H. dyacorum* and its palation lacks a median emargination : it has a wider mesopterygoid fossa and wider, more spreading pterygoids, with an unconstricted sphenoidal bridge. The affinities of *H. breviceps* clearly lie with *H. galeritus*, from which it differs in a number of cranial features, such as its relatively shorter skull and less well-defined supraorbital ridges, slightly more inflated rostral eminences, shorter premaxillae, shorter palate and strongly convergent upper incisors. It is approached most nearly by *H. g. schneideri*, which closely resembles *H. breviceps* and has a similarly shortened skull, but which is larger and has rather more prominent supraorbital ridges, less inflated rostral eminences and longer premaxillae. The dentition of *H. g. schneideri* is almost identical with that of *H. breviceps*, with the anterior upper premolar (pm^2) minute or absent and the anterior lower premolar (pm_2) much reduced. The upper incisors of *H. g. schneideri*, however, are much less strongly convergent at their tips than in *H. breviceps*, in which the tips almost touch, and the anterior lower premolar (pm_2) is slightly less reduced. The majority of its characters indubitably ally *H. breviceps* closely to *H. galeritus*, with which it is apparently sympatric in the Mentawei Islands (Tate (1941 : 368, 391) records *H. g. schneideri* from North Pagi Island) and it is considered to be a recently derived species, close to *H. galeritus* and having much the same relationship to that species as *H. beatus* has to *H. caffer* in the Ethiopian region.

DISTRIBUTION : Mentawei Islands : North Pagi Island.

Hipposideros curtus G. M. Allen

Hipposideros curtus G. M. Allen, 1921 : 194. Sakbayème, Cameroons.
Hipposideros sandersoni Sanderson, 1937 : 290, 296. Near Mamfe, Nigeria.

The ears are very large and broad, rather rounded and bluntly pointed, with a sharp concavity behind the tip. There is a small antitragal fold and they are haired for one half their length. The noseleaf is broad, with two small lateral supplementary leaflets. The anterior leaf has a small median emargination. The internarial septum is swollen and inflated, especially posteriorly between the nostrils, where it forms a slightly disc-like structure, the disc not however concealing the nostrils. The intermediate part of the leaf is cushion-like, with a low median eminence. The posterior leaf is high, its upper edge semicircular, and is supported by three septa enclosing deep pockets. A frontal sac is present in both sexes.

The skull is small, short and broad, with a low sagittal crest. The interorbital region is moderately constricted, with ill-defined supraorbital ridges. The frontal region is more or less pentagonal as in *H. galeritus*, with a shallow frontal depression and well-inflated rostral eminences separated by a shallow groove. The zygomata are moderate with a low jugal projection and the anteorbital foramen is large and rounded, closed by a narrow bar. The premaxillae make a V-shaped junction with the maxillae and the palate is short, with a square palation. The mesopterygoid fossa is wide with a slightly projecting vomer, while the pterygoids are short, with a narrow, sharply constricted sphenoidal bridge exposing slightly elongate lateral apertures. There is a very shallow sphenoidal depression and the width of the cochleae is equal to their distance apart or is very slightly greater. The upper incisors are weakly bilobed and the upper canines shallowly grooved anteriorly, with low anterior and posterior cusps. The anterior upper premolar (pm^2) is small, slightly extruded but compressed between the canine and the second upper premolar (pm^4). The posterior ridge of the third upper molar is much reduced and obsolescent. The crown area of the outer lower incisors is a little greater than that of the inner lower incisors, while the anterior lower premolar (pm_2) is considerably reduced, to one half the length and one third the height of the second lower premolar (pm_4).

Hipposideros curtus, like *H. fuliginosus*, is a species evidently derived from the *bicolor-caffer* line and presents features which ally it to both the *bicolor* and *galeritus* sections of the *bicolor* group. Its external characters, especially the form of the ears, demonstrate its affinity to the *bicolor* subgroup but its short, broad skull tends towards the *galeritus* subgroup while *H. curtus* has also the short pterygoids and narrow sphenoidal bridge characteristic of *H. caffer* and its immediate allies.

DISTRIBUTION : West Africa : Cameroons ; Nigeria.

Hipposideros fuliginosus (Temminck)

Phyllorrhina fuliginosa Temminck, 1853 : 77. " La côte de Guiné ".

The ears are large and broad, sharply triangular and acutely pointed, with a slight trace of an internal fold. Their posterior margins are slightly concave behind the tip, and they are haired for one half of their length. The noseleaf is comparatively broad, with two lateral supplementary leaflets, the anterior leaflet extending anteriorly for a short distance below the anterior leaf. The anterior leaf is simple with the internarial septum uninflated and with well-developed narial lappets. The intermediate part of the leaf is inflated, with a low median eminence. The posterior leaf is high, its upper edge semicircular and unlobulated. It lacks supporting septa but has a very low transverse structure, its upper edge not serrated, developed from its posterior face. There is no trace of a frontal sac in two male specimens (see also Hayman (1946 : 772)).

The skull is elongate, with a low to moderate sagittal crest. The interorbital region is long and relatively unconstricted, with barely defined supraorbital ridges. There is no frontal depression and the rostral eminences are moderately inflated and separated by a shallow trough. The zygomata are slender with a moderate jugal projection and the anteorbital foramen is elongate and closed by a narrow bar. The anterior palatal foramina are elongate and not enclosed by the premaxillae, which make a V-shaped junction with the maxillae. The palation is square with a shallow median emargination. The mesopterygoid fossa is wide with long, moderately expanded pterygoids which partially conceal elongate lateral apertures. The sphenoidal bridge is moderately constricted and there is a moderate sphenoidal depression. The cochleae are rather less in width than their distance apart. The upper incisors bear only a trace of the outer lobe and the upper canines have a shallow groove on their anterior faces, with weak anterior and posterior cusps. The anterior upper premolar (pm^2) is much reduced, extruded, with the canine and the second upper premolar (pm^4) almost in contact. The posterior ridge of the third upper molar is one third the length of the anterior ridge. The crown area of the outer lower incisors slightly exceeds that of the inner lower incisors, and the anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4).

There is little doubt that *H. fuliginosus* is a derivative of the line leading from *H. bicolor* and its allies to the more specialized *H. caffer*, possessing certain features common to the *bicolor* subgroup and others common to the *galeritus* subgroup, to which *H. caffer* is allocated. It has broad, sharply triangular ears, two lateral supplementary leaflets and the posterior leaf, which lacks supporting septa, has a low transverse structure developed from its posterior face. These features ally it to *H. caffer*: however, its skull is elongate with the long interorbital region characteristic of the members of the *bicolor* subgroup.

DISTRIBUTION: West Africa: Liberia; Togo; Ghana; Nigeria; Cameroons; Gaboon; Congo.

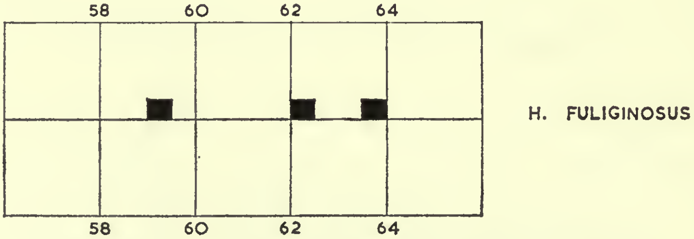


FIG. 14. Length of forearm in *Hipposideros fuliginosus*

Hipposideros caffer

The ears are large, broad, triangular and acutely pointed. Their posterior margins are concave just behind the tip. There is a slight thickening at the antitragal fold and the ears are haired for two thirds to three quarters of their length. The noseleaf is comparatively simple with two lateral supplementary leaflets, the anterior leaflet extending anteriorly beneath the anterior leaf, sometimes reaching or almost reaching the median line. The anterior leaf is simple and has no median emargination. The internarial septum is slightly inflated. The intermediate part of the leaf is cushion-like, with a low to moderate median eminence, sometimes with low lateral eminences. The posterior leaf is thin, its upper edge semicircular, unlobulated and lacks supporting septa. Its posterior face bears a transverse supplementary structure with a serrated upper edge below that of the true posterior leaf. A frontal sac is present in both sexes but is very small in females.

The skull is short and broad, closely similar in outline to the skull of *H. galeritus*. The braincase is broad with a low sagittal crest and the interorbital region is not greatly constricted, the supraorbital ridges low but sharply defined. There is no frontal depression and the rostral eminences are moderately inflated. The zygomata have a high jugal process, set far back, and the anteorbital foramen is elongate, closed by a narrow bar. The premaxillae make a U-shaped or shallowly V-shaped junction with the maxillae and the anterior palatal foramina are slightly elongate, not enclosed within the premaxillae but almost closed posteriorly by the delicate anterior enclosing processes. The palation is nearly square with a small median notch while the mesopterygoid fossa is wide, the vomer not projecting and the pterygoids short, with a narrow, sharply constricted sphenoidal bridge exposing wide lateral apertures. There is a shallow sphenoidal depression. The cochleae are moderate, their width equal to or a little greater than their distance apart. The upper incisors are weakly bilobed, their outer lobes obsolescent. The upper canines have their anterior faces flattened or with a shallow, ill-defined groove and have a moderate anterior cusp and a slightly higher posterior cusp. The anterior upper premolar (pm^2) is small or very small, slightly extruded, compressed between the canine and the second upper premolar (pm^4), which usually are not in contact, sometimes more fully extruded with these teeth in contact or nearly so. The posterior ridge of the third upper molar is not greatly reduced, equal to one half the length of the anterior ridge or more. The crown area of the outer lower incisors is very slightly greater than that of the inner pair. The anterior lower premolar (pm_2) is not excessively reduced, one half or more the length and height of the second lower premolar (pm_4).

Hipposideros caffer is the principal representative of the *galeritus* subgroup in the Ethiopian region, and like *H. galeritus*, is the dominant and most widely distributed species of the subgroup in its region. Despite its superficial resemblance to *H. galeritus*, it differs widely from this and its associated species in the structure of its posterior noseleaf and in the characters of the post-palatal region. These differences suggest remote origin in the *bicolor* group although there seems little doubt that *H. galeritus* and *H. caffer* have developed from a common if remote source. Both are similarly specialized in a number of features, notably in the extent of body fur on the ears and in the number of lateral supplementary leaflets : both have a characteristic short broad skull very different from the elongate narrow skull of the *bicolor* type yet both can be linked to the *bicolor* subgroup by a series of species exhibiting a variety of features on the one hand found in *bicolor* and *galeritus* and on the other in *bicolor* and *caffer*.

A number of subspecies have been proposed to divide *H. caffer*, mainly on the basis of size, and there is considerable dimensional overlap between them. No attempt has been made in the present work to establish the validity of the named forms of *H. caffer* but there seems little doubt from the very large series from most parts of its range now preserved in the collections of the British Museum (Natural History) that the variation in size of the species is largely clinal. Smaller subspecies (*H. c. caffer, H. c. tephrus*) are found in the Yemen, in the eastern part of Africa, in North Africa and on the west coast south to Sierra Leone and the Gold Coast. A larger subspecies (*H. c. ruber*) replaces *H. c. caffer* in the west of Kenya, Uganda and Tanganyika, extending westwards through the Congo, to be itself replaced in west Africa by another large subspecies (*H. c. guineensis*) and in Angola and southwest Africa by yet another large subspecies (*H. c. angolensis*). The distributional limits of the subspecies are difficult of definition, and series from some localities cannot be allocated with certainty to subspecies.

DISTRIBUTION : Yemen ; the greater part of Africa excluding the Sahara desert and the extreme south.

Hipposideros caffer caffer (Sundevall)

Rhinolophus caffer Sundevall, 1846 : 118. Near Port Natal.
Phyllorrhina gracilis Peters, 1852 : 36, pl. 7, figs. 1–4, pl. 13, figs. 14–15. Tette, Lower Zambezi, Mozambique.
Phyllorrhina bicornis Heuglin, 1861 : 4, 7. Kérén, Eritrea.

DISTRIBUTION : Yemen ; Eritrea ; Somaliland ; Sudan ; Ethiopia ; Kenya (part) ; Tanganyika (part) ; Southern Rhodesia ; Northern Rhodesia (part) ; Nyasaland ; Natal ; Transvaal ; Zanzibar ; Pemba Island; Congo (part).

Hipposideros caffer tephrus Cabrera

Hipposideros tephrus Cabrera, 1906 : 358. Mogador, Morocco.
Hipposideros braima Monard, 1939 : 73, fig. 5. Bagingara, Portuguese Guinea (see Aellen (1956b : 26)). *Hipposideros braima* is further described and illustrated by Veiga-Ferreira (1949 : 193).

DISTRIBUTION : North Africa : Morocco ; Senegal (part) ; Nigeria (part) ; Sierra Leone (part) ; Ghana (part) ; Senegambia.

Hipposideros caffer ruber (Noack)

Phyllorhina rubra Noack, 1893 : 586, pl. 18, figs. 14–15. " Lugerrunjere Fluss ", Tanganyika.
Hipposideros caffer centralis Andersen, 1906b : 275, 277. Entebbe, Uganda.

DISTRIBUTION : Tanganyika (part) ; Kenya (part) ; Uganda ; Congo (part) ; North Rhodesia (part) ; Angola (part) (Sanborn (1950 : 58)) ; recorded from Guinea by Aellen (1956a : 889).

Hipposideros caffer angolensis (Seabra)

Phyllorhina angolensis Seabra, 1898 : 256. Rio Coroca, Angola.

DISTRIBUTION : Angola ; southwest Africa ; Gaboon (part) ; recorded from Ghana by Booth (1956 : 137).

Hipposideros caffer guineensis Andersen

Hipposideros caffer guineensis Andersen, 1906b : 275, 278. Como River, 70 miles from Gaboon.

DISTRIBUTION : Gaboon (part) ; Cameroons ; Nigeria (part) ; Ghana (part) ; Gambia ; Sierra Leone (part) ; Liberia ; San Thomé Island ; Principe Island ; Fernando Po ; Spanish Guinea ; Senegal (part) (Aellen (1956b : 26)).

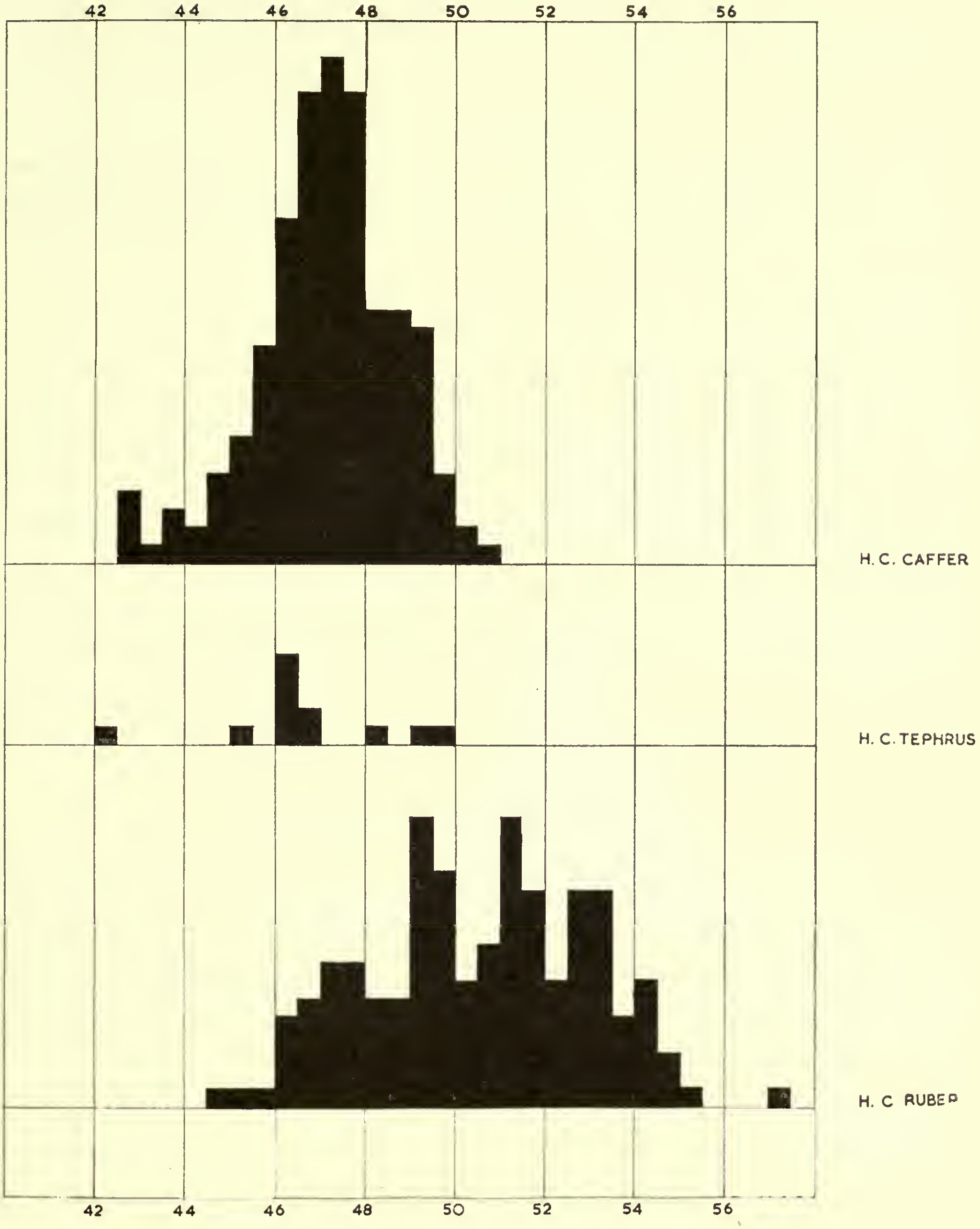


FIG. 15. Length of forearm in *Hipposideros caffer*

Hipposideros caffer niapu J. A. Allen

Hipposideros caffer niapu J. A. Allen, 1917 : 431. Niapu, northeastern Congo.

DISTRIBUTION : Congo (part).

Hipposideros beatus

The ears are large, broad, triangular and pointed. Their posterior margins are concave just behind the tip. There is a slight thickening at the antitragal fold and they are haired for two thirds of their length. The noseleaf exactly resembles

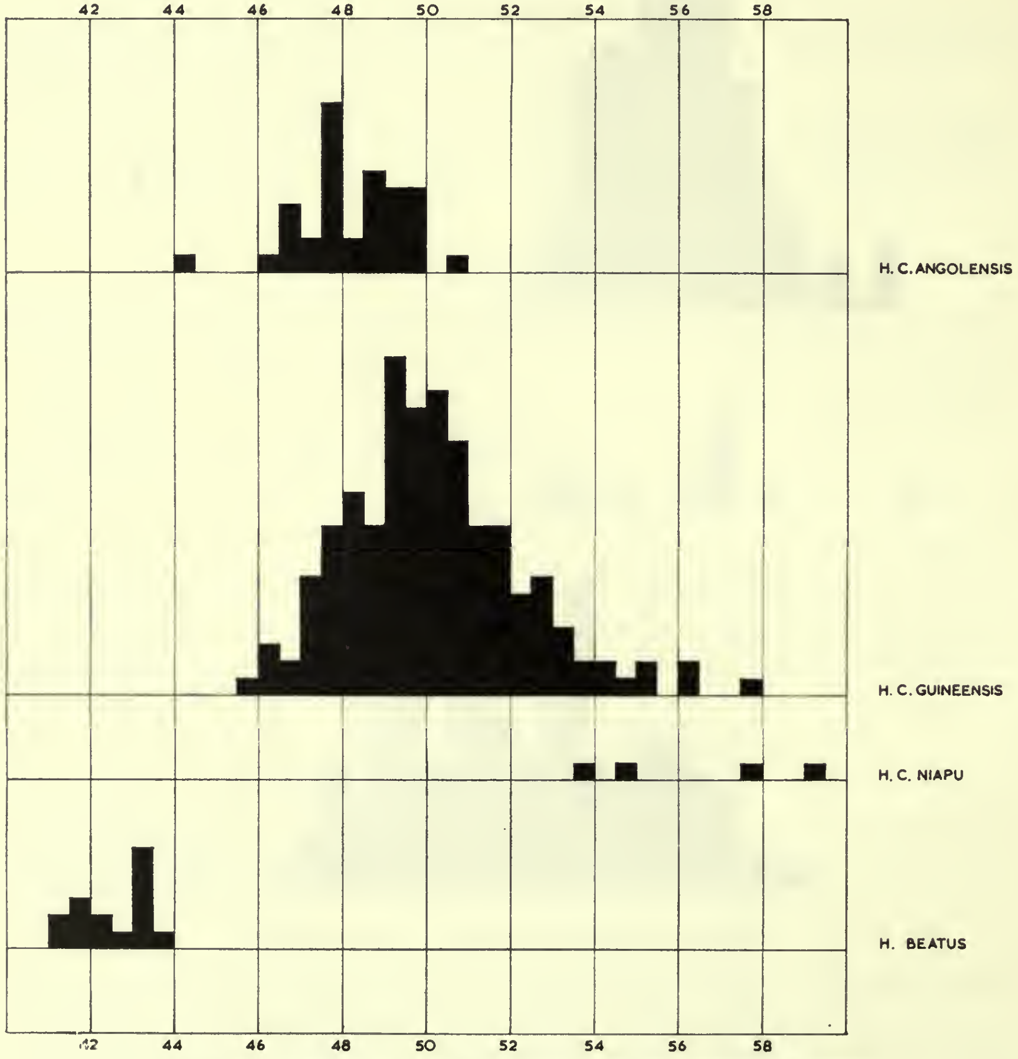


FIG. 16. Length of forearm in *Hipposideros caffer* and *H. beatus*

that of *H. caffer*. The skull is short and broad and very similar to that of *H. caffer*. There is a low sagittal crest and the interorbital region is only slightly constricted, with low but sharply defined supraorbital ridges. There is a very shallow frontal depression and the rostral eminences are inflated and separated by a shallow groove. The zygomata are slender, with a high jugal process, and the anteorbital foramen is rounded, closed by a narrow bar. The premaxillae make a V-shaped junction with the maxillae and the palation is square with a median notch. The mesopterygoid fossa is a little narrower than in *H. caffer*, the pterygoids short with a narrow, sharply constricted sphenoidal bridge exposing wide lateral apertures. There is a shallow sphenoidal depression and the width of the cochleae is equal to their width apart or is slightly greater. The upper incisors are weakly bilobed and the upper canines have a weak anterior cusp and a low but well developed posterior cusp. The anterior upper premolar (pm^2) is minute, extruded, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is one third or less the length of the anterior ridge. The crown area of the outer lower incisors is slightly greater than the crown area of the inner pair. The anterior lower premolar (pm_2) is a little more than one half the length and height of the second lower premolar (pm_4).

Hipposideros beatus differs only very slightly from *H. caffer*, and may be distinguished from that species chiefly by its smaller size and the greater degree of reduction of its anterior lower premolar (pm_2). The two species provide an interesting parallel in the Ethiopian region to the Asiatic species *H. galeritus* and *H. breviceps*, the latter differing only very slightly from the former. *Hipposideros beatus* is slightly more advanced than *H. caffer* in the details of its dentition and is regarded as a very close derivative of *H. caffer*.

DISTRIBUTION : West Africa from the Congo to Sierra Leone.

Hipposideros beatus beatus Andersen

Hipposideros beatus Andersen, 1906b : 279. 15 miles from Benito River, West Africa.
Hipposideros nanus J. A. Allen, 1917 : 434. Faradje, Uele District, eastern Congo.

Hayman (1936 : 919) thought that *H. nanus* Allen probably referred to the dark phase of *H. beatus*. Verschuren (1957 : 371) considered it to be a distinct species, distinguished chiefly by its colour and by the insertion of the wing membrane on the tibia and not on the metatarsals as in *H. beatus*. These features are variable in a small series of *H. beatus* and for the present *H. nanus* is provisionally retained in the synonymy of this species.

DISTRIBUTION : Congo (part) ; Cameroons ; Nigeria ; Ghana ; Liberia ; Sierra Leone.

Hipposideros beatus maximus Verschuren

Hipposideros beatus maximus Verschuren, 1957 : 362, 365. Pidigala-Nord, Parc National de la Garamba, Congo.

Hipposideros coxi Shelford

(Figure 17)

Hipposideros coxi Shelford, 1901 : 113. Mount Penrisen, Sarawak, Borneo, 4,200 feet.

A species of medium size with very large, sub-triangular ears, broad at the base, bluntly pointed, with their anterior margins slightly concave in the upper portion, their posterior margins strongly so for the upper third, thereafter convex. The antitragal lobe is well developed, with a prominent internal fold, and the ears are haired for two thirds of their length. The noseleaf is large and forms a structure of extraordinary complexity, covering the entire muzzle, with two lateral supplementary leaflets. The anterior leaflet on each side extends anteriorly beneath the anterior leaf to become continuous over the upper lip, with no median emargination. At its upper or posterior end this leaflet terminates on each side in a small wart-like protuberance or papilla, at about the level of the eye, pierced by a minute pore. A small, sharply triangular pointed leaflet extends upwards from this papilla behind the lateral margin of the anterior leaf. This extension of the anterior supplementary leaflet at its upper end joins a further cutaneous leaflet extending from the rear of the intermediate part of the leaf, to which it is attached, downwards to a point just above the eye, forming a structure of the shape of an inverted Y. The lateral margin of the posterior leaf is joined to the upper surface of this cutaneous leaflet : the junction of the triangular extension of the supplementary leaflet is on its lower surface at a point nearer to the eye, these leaflets enclosing deep pockets behind the intermediate part of the leaf. Cutaneous outgrowths composed either of the anterior lateral supplementary leaflet or of extensions therefrom thus extend completely beneath the anterior leaf and beneath much of the margins of the intermediate part of the leaf, forming deep pockets beneath the latter. The posterior lateral supplementary leaflet is broad and extends from a point level with the wart terminating the anterior leaflet only for a short distance on to the muzzle, just reaching the upper lip. This observation is contrary to that of Shelford, who stated in the original description that the lower (or posterior) leaflet consisted of two separate parts : it is clear from the type specimen, however, that Shelford mistook the cutaneous leaflet extending downwards from the base of the posterior leaf to be a part of the posterior leaflet, but it is apparently a structure quite distinct from either of the lateral supplementary leaflets. The anterior leaf is very large, lacking a median emargination, completely covering the muzzle and with its margin projecting beyond the upper lip and concealing the anterior lateral supplementary leaflets, which however project beyond the lateral margins of the anterior leaf. The internarial septum is slightly bulbous anteriorly, dividing two deep pockets anterior to the nostrils. The narial region is greatly specialized, the narial lappets greatly developed and with their bases expanded towards the median line to join the internarial septum, forming deep pouches at the base of which the nostrils are situated. These pouches have slightly crescentic, elongate openings and the narial lappets project above the level of the anterior leaf. The intermediate part of the leaf is inflated with a prominent median ridge, sparsely haired at its upper end :

laterally, there are two low eminences on each side of this ridge, just beneath the upper margin of the intermediate part of the leaf. The lateral margins of the intermediate part of the leaf are extended laterally to form a triangular lappet on each side extending over the bases of the margins of the anterior leaf and over the bases of the lateral supporting septa of the posterior leaf. The posterior leaf is very high, thick, its upper edge rounded and is supported by three septa. The central or median septum is narrow and blade-like, with a large, deep cell flanking it on each side. The lateral septa are very broad, their upper ends continuous with the face of the posterior leaf, the cells external to these septa narrow but very deep. The upper third of the posterior leaf extends above these septa and in the type specimen (in alcohol) is folded back upon itself. Laterally, the margins of the posterior leaf extend downwards and are joined to cutaneous leaflets attached on each side to the rear of the lateral lappets of the intermediate part of the leaf. At their upper ends these leaflets form the floor of the deep lateral cells of the posterior leaf and the roof of deep pockets beneath the intermediate part of the leaf.

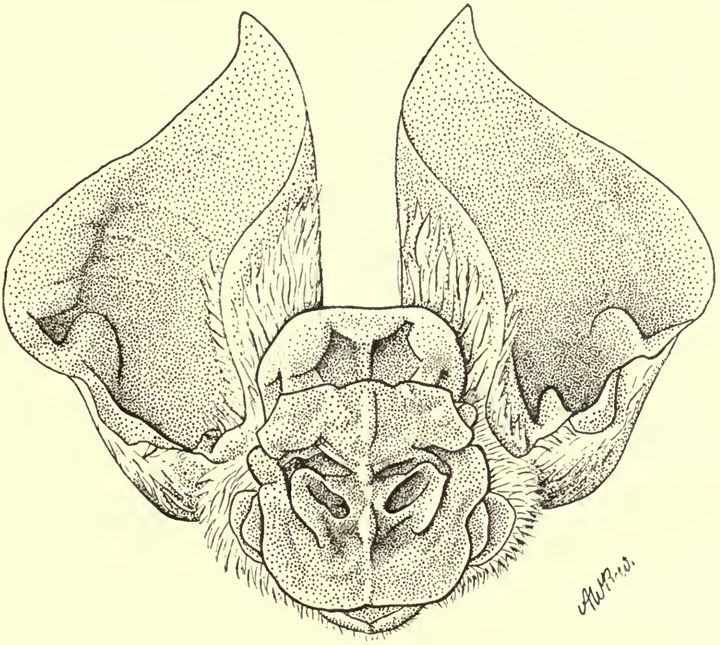


Fig. 17. *Hipposideros coxi* ♀ (Type B.M. 1.6.23.1) (x3)

The skull is elongate and comparatively narrow, with an elongate braincase and low sagittal crest. The interorbital region is not sharply constricted and there are no supraorbital ridges. There is no frontal depression and the rostrum is elongate and high, with the rostral eminences much inflated, separated by a shallow depression. The zygomata are slender with a low jugal projection and the zygomatic width is less than the mastoid width. The anteorbital foramen is small and rounded, separated from the orbit by a massive bar of bone enclosing a long anteorbital canal.

The premaxillae of the type specimen are missing. The palate is not markedly shortened, the palation shallowly V-shaped with a small post-palatal spicule. The mesopterygoid fossa is wide, the vomer not projecting, with long, expanded pterygoids and wide sphenoidal bridge almost concealing narrow, elongate lateral apertures. There is a shallow sphenoidal depression and the width of the cochleae slightly exceeds their distance apart. The upper canines have low anterior and posterior cusps and the anterior upper premolar (pm^2) is very small, extruded from the toothrow, with the canine and the second upper premolar (pm^4) almost in contact. The second anterior upper premolar (pm^4) has a well-developed anterior cusp. The posterior ridge of the third upper molar is one half the length of the anterior ridge. The crown area of the outer lower incisors slightly exceeds that of the inner pair and the anterior lower premolar (pm_2) is slightly over one half the length of the second lower premolar (pm_4) and is one half of its height.

Hipposideros coxi is very sharply removed from the other species of the *bicolor* group by the great specialization of its noseleaf, which in the degree of its complexity is approached by no other species of the group. Certain features, however, ally it to the *bicolor* group. Its ears are of the *bicolor* type, with a well-developed internal fold. The anterior lateral supplementary leaflet extends beneath the anterior leaf to reach the median line : a similar condition is found in *H. jonesi* and *H. pygmaeus*, which have the leaflets divided above the centre of the upper lip by a deep emargination. There is no such emargination in *H. coxi*, and the anterior lateral supplementary leaflets form an uninterrupted cutaneous frill beneath the anterior leaf. Narial pockets surrounding the nostrils, greatly developed in *H. coxi*, are less pronounced in *H. pygmaeus* and are developed to some extent in *H. obscurus*. The elongate skull and narrow zygomata of *H. coxi* demonstrate its affinity to the *bicolor* subgroup, but its complex noseleaf and long anteorbital canal, enclosed by a massive bar of bone, clearly remove it from any close relation to the members of this subgroup or of the *galeritus* subgroup. Its great degree of specialization suggests that *H. coxi* must be considered an isolated species of remote origin and it is probably derived from the basal stem of the *galeritus* subgroup.

Hipposideros papua (Thomas & Doria)
(Figure 18)

Phyllorhina papua Thomas & Doria, 1886 : 204. Korido, Misori Island, Geelvinck Bay, Netherlands New Guinea.

(?) *Phyllorhina cervina* var. *misorensis* Peters, 1906: pl. 5L, figs. 4, 4a, 4b.

The ears are long, broad and triangular, acutely pointed, their posterior margins forming a smooth convex curve. There is a small, slightly thickened antitragal fold and the ears are apparently haired for one third or a little more, perhaps one half of their length (the syntype and only available specimen has the skin in bad condition). The noseleaf is broad, covering the entire muzzle, with three lateral supplementary leaflets, the first normal, extending upwards to the base of the posterior leaf just anterior to the eye, the central or second leaflet extending from a point below and just anterior to the eye anteriorly beneath the anterior leaf on to the upper lip but not reaching the median line and the third leaflet very small, rudimentary and incipient. The anterior leaf is large, extending over the upper lip, but has no median emargination. The internarial septum is uninflated and the narial lappets well developed, with the internarial septum forming shallow narial pockets. The intermediate part of the leaf is simple with a low median ridge. The posterior leaf is high, its upper edge semicircular and thickened and is supported by three moderate septa enclosing shallow pockets. There is a small depression but no frontal sac in the female type specimen.

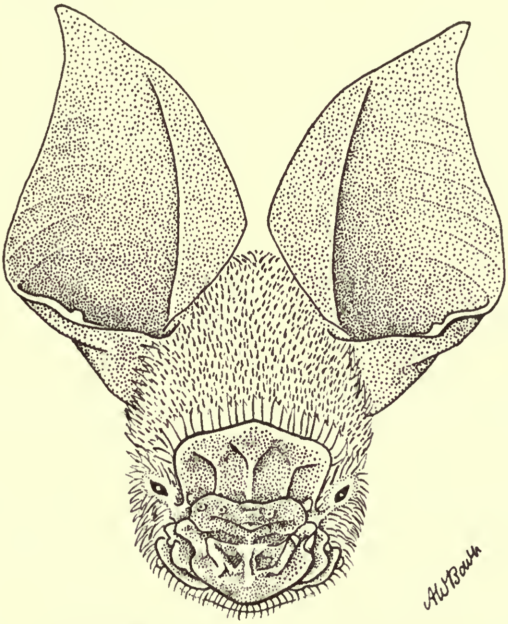


Fig. 18. *Hipposideros papua* ♀ (Syntype B.M. 86.11.3.9) (x3)

The skull is only slightly elongate, with a long, broadened braincase and moderate sagittal crest. The interorbital region is moderately constricted with barely defined supraorbital ridges. There is a moderate frontal depression, and the rostrum is slightly broadened, with well-inflated rostral eminences separated by a shallow groove. The zygomata are slender, with a moderate jugal process, and the anteorbital foramen is large, elongate and closed by a narrow bar. The premaxillae make an acutely V-shaped junction with the maxillae and the anterior palatal foramina are elongate and not totally enclosed. The palate is not markedly shortened, the palation U-shaped with a small post-palatal spicule. The mesopterygoid fossa is moderate and not greatly widened, the vomer not projecting and the pterygoids long with a wide sphenoidal bridge, almost completely concealing elongate lateral apertures. There is a moderate sphenoidal depression and the width of the cochleae is slightly greater than their distance apart. The upper incisors are not bilobed and the upper canines have low anterior and posterior cusps. The anterior upper premolar (pm^2) is small and is only slightly out of alignment in the toothrow.

The posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is equal to that of the inner pair and the anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4).

Tate (1941 : 369, 387) was uncertain of the taxonomic position of *H. papua* and regarded it as a perplexing species. Its ears and cranial characters suggest affinity with the *bicolor* group, but *H. papua* has a specialized noseleaf which indicates no close connection with any of the members of that group. Some affinity to the *cyclops* group is suggested by the extension of the second lateral leaflet beneath the anterior leaf, a feature otherwise peculiar to *cyclops* and its allies, but *H. papua* differs from these in its broad ears, the presence of an incipient third leaflet, unenlarged bullae and convergent toothrows. A more tenuous affinity to the *speoris* group may be indicated by the presence of a rudimentary third leaflet. For the present *H. papua* must be regarded as a species of remote origin within the *bicolor* group, associated probably with the line leading to the *muscinus* group and less certainly with that leading to the *speoris* group.

HIPPOSIDEROS CYCLOPS group

The *cyclops* group as here understood includes the *cyclops* and *muscinus* groups of Tate (1941), both characterized by the great development of the ears and auditory region. The group includes six species, *H. cyclops*, *H. camerunensis*, *H. muscinus*, *H. wollastoni*, *H. semoni* and *H. stenotis*, all demonstrating a high degree of modification and specialization. The ears are long, narrow and acutely pointed, lacking any antitragal modification and not extensively haired. The noseleaves are much specialized, with two lateral supplementary leaflets. The anterior lateral supplementary leaflet is small, the posterior leaflet larger, extending posteriorly to the base of the posterior leaf, of which it forms a continuous part and in the majority of species extending anteriorly beneath the anterior leaf. The anterior leaf has no median emargination and the internarial septum is uninflated or only slightly thickened. The intermediate part of the leaf is flat or slightly cushion-like, specialized by the development to a greater or lesser degree of a median tubercle. The posterior leaf is moderate, with three supporting septa, its upper edge more or less semicircular, thickened, usually with a median club-like process (*H. cyclops*, *H. camerunensis*, *H. muscinus*, *H. semoni*, *H. stenotis*) or with a transverse supplementary structure developed from the posterior face of the leaf (*H. wollastoni*). The frontal sac is usually absent.

The skull is short and broad, the braincase wide and almost globose, with a low sagittal crest. The interorbital region is much constricted, with low supraorbital ridges. The rostrum is greatly broadened, with well-inflated rostral eminences. The zygomata are slender or moderate, with a low jugal process, and the anteorbital foramen is rounded, closed by a narrow bar, or pore-like. The palate is short and the pterygoids are long, together with the wide sphenoidal bridge almost concealing elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are greatly developed, their width equal to four or more times their distance apart. The outer lobe of the upper incisors is obsolescent or absent and the upper canines in most cases lack cusps but have well-developed cingula. The anterior upper premolar (pm^2) is usually much reduced and is absent in one species. The posterior ridge of the third upper molar is obsolescent or well developed, in some species almost complete with the W-pattern of the tooth virtually complete. The anterior lower premolar (pm_2) is much reduced.

The group is one of restricted distribution, with two species in the Ethiopian region and the remainder in New Guinea and northern Australia. As might be expected from this markedly discontinuous range, the group can be divided readily into two sharply defined sections, corresponding to the *cyclops* and *muscinus* groups of Tate (1941). Despite this sharp division, the two sections share features in common that make their independent origin unlikely. Their specialized ears and auditory region are unknown elsewhere in *Hipposideros*, as is the rearward extension of the posterior lateral supplementary leaflet to form a continuous part of the posterior leaf. The noseleaves are further specialized by the development of club-like projections, of which Tate (1941 : 379) observes that they are " structures so peculiar, specialized and seemingly functionless that they are unlikely to have arisen independently ". The two sections share further the same typically shortened, broadened pattern of skull, unwidened at the mastoid region and with wide pterygoids and greatly enlarged cochleae.

The Ethiopian species *H. cyclops* and *H. camerunensis* are clearly the most primitive members of the group and may be readily distinguished from the Australasian species *H. muscinus*, *H. wollastoni*, *H. semoni* and *H. stenotis* by their much larger size. Their noseleaves differ markedly from those of the Australasian species in that the posterior lateral supplementary leaflet does not extend anteriorly beneath the anterior leaf, while the skulls of the Ethiopian species are more elongate than those of *H. muscinus* and its allies. The interorbital region is less sharply constricted in the Ethiopian species, and the rostral swellings, although inflated, are less swollen and more ossified. The premaxillae are wide and completely enclose narrow, elongate anterior palatal foramina, making a broad junction with the maxillae extending over almost the entire width of the palatal emargination in contrast to the narrow premaxillae of the Australasian species, which do not enclose the large oval anterior palatal foramina and which make a narrow junction with the maxillae, extending over only one third of the width of the palatal emargination. The cochleae are large but are less developed than those of the Australasian species, and are equal in width to approximately four times their distance apart.

Hipposideros muscinus and its allies, confined to New Guinea and northern Australia, are much smaller and more specialized than *H. cyclops* and its close relative *H. camerunensis*. The noseleaves of the Australasian species are characterized by a number of specializations, among which the forward extension of the posterior lateral supplementary leaflet beneath the anterior leaf is the most noticeable. These species have the skull much shortened, especially in the rostral region, with a broad braincase and a constricted interorbital region. As in *H. cyclops* and *H. camerunensis*, the inflated braincase is not abruptly widened at the level of the mastoids. The interorbital region is short and much less elongate than in *H. cyclops* and *H. camerunensis*, while the rostrum, although broadened, is rounded and less angular. As in *H. cyclops* and *H. camerunensis*, the Australasian species have long pterygoids and a wide sphenoidal bridge, but the cochleae are more greatly expanded, their width in the majority of species equal to six or more times their distance apart. These differences suggest comparatively remote separation of the parental stocks of the two sections : *H. cyclops* and *H. camerunensis* have retained to some extent the elongate outline of the skull typical of the *bicolor* group, particularly in the elongate, broadened braincase, although the rostrum and palate are shortened, while *H. muscinus* and its allies are rather more specialized and represent a further trend of modification within the group.

Although *H. muscinus*, *H. wollastoni*, *H. semoni* and *H. stenotis* are closely related, it is possible to discern a weak division among them. *Hipposideros muscinus* is the least specialized : the tubercles on its intermediate and posterior noseleaves are not greatly developed, it lacks a frontal depression, its anteorbital foramen is elongate, closed by a narrow bar, there is a shallow sphenoidal depression traversed by a low median ridge and its cochleae are the least expanded, in width equal to approximately four to five times their distance apart. The anterior upper premolar (pm²) is not greatly extruded and the posterior ridge of the third upper molar is small, less than one third the length of the anterior ridge, with the W-pattern of the tooth incomplete. *Hipposideros wollastoni*, despite the divergence of its posterior noseleaf, is cranially very similar to *H. muscinus*. However, its rostral eminences are rather more swollen, its anteorbital foramen is rounded, closed by a narrow bar, the sphenoidal bridge is less constricted, the sphenoidal depression not traversed by a median ridge and the cochleae more expanded, their width equal to six times their distance apart. The anterior upper premolar (pm²) is small, extruded and the posterior ridge of the third upper molar is less reduced, one third or a little more the length of the anterior ridge, with the W-pattern of the tooth less incomplete.

Hipposideros semoni and *H. stenotis* are more closely related to each other than to *H. muscinus* or *H. wollastoni*, although their affinities as demonstrated by the noseleaves clearly lie nearer to *H. muscinus* than to *H. wollastoni*. In both *H. semoni* and *H. stenotis* the tubercles on the intermediate and posterior noseleaves are developed into club-like processes similar to those of *H. cyclops*. Cranially, both have a frontal depression and the anteorbital foramen is small and rounded, closed in *H. semoni* by a moderate bar and in *H. stenotis* by a narrow bar. In both the sphenoidal bridge is slightly more constricted than in *H. muscinus* or *H. wollastoni*. Neither *H. semoni* nor *H. stenotis* has a sphenoidal depression and in both the cochleae are greatly expanded, their width equal to eight times their distance apart. In *H. semoni* the anterior upper premolar (pm²) is small and extruded from the toothrow : it is absent in *H. stenotis* while in both the posterior ridge of the third upper molar is not greatly reduced and is equal nearly in length to the anterior ridge, the W-pattern of the tooth nearly complete. In view of these considerations I am unable to agree with Tate (1941 : 379) that there can be no doubt that *H. muscinus*, *H. semoni* and *H. stenotis* are conspecific : although the available material is limited, it is evident that *H. muscinus* is widely separated from *H. semoni* and *H. stenotis*, although these by comparison are closely related, as Tate (p. 389) recognized.

Tate (1941 : 378, 379) has provided an account of the *muscinus* group as he understood it, evidently based on series from various localities in Papua which he considered to represent *H. muscinus* (pp. 379, 386, 392). Furthermore, he notes (p. 386) that " there is no doubt that *muscinus* is very closely related to *semoni* and *stenotis* " and after reviewing some of the features of the ears and noseleaf of *H. muscinus* as given by Thomas & Doria in the original description states that the skull, which they did not describe, as represented by the syntype in the British Museum (Natural History) " shows the characteristics of *semoni* and agrees with my topotypical series of *muscinus* : the parallel toothrows, the greatly enlarged rostrum, the closely approximated cochleae, etc.". A comparison of his detailed account (pp. 378, 379) with the syntype of *H. muscinus* in the British Museum (Natural History) suggested that the specimens that Tate used as the basis of his study and that he referred to *H. muscinus* in fact did not represent that species but should be referred to *H. semoni*. Through the courtesy of the authorities of the American Museum of Natural History I have been able to examine a part of this series of specimens, including three of those from the Fly River, Papua, thought topotypical of *H. muscinus* by Tate. Comparison of this selection of the specimens studied by Tate with the syntype of *H. muscinus* and with examples of *H. semoni* in the collections of the British Museum (Natural History) shows that without doubt they represent the latter species.

A specimen preserved in alcohol, A.M.N.H. 108684, a male from the bank of the Fly River, opposite Sturt Island, Papua, has the noseleaf as described by Tate, its intermediate and posterior leaves with club-shaped median protuberances. These can be readily discerned in four other dry skins from Papua, A.M.N.H. 105341, a female from the same locality ; A.M.N.H. 105057, a male from five miles below Palmer Junction, Upper Fly River ; A.M.N.H. 108500, a young female from Baruari, Astrolabe Range, Central Division and A.M.N.H. 108504, a male from Sogeri, Central Division. These protuberances in the syntype of *H. muscinus* are not developed into club-shaped structures as in *H. semoni* and *H. stenotis* but take the form of tubercles. The skulls of the four dry specimens are available for study and agree exactly with the account by Tate. All have a small frontal depression, absent in *H. muscinus* but present in *H. semoni*. The anteorbital foramen is small, rounded and separated from the orbit by a moderate bar as in *H. semoni* : in *H. muscinus* this aperture is not rounded but is elongate and is separated from the orbit by a narrow bar. There is a low median sphenoidal ridge and no sphenoidal depression as in *H. semoni* : a shallow sphenoidal depression is present in *H. muscinus*. The cochleae are very large, their width equal to six or eight times their distance apart as in *H. semoni* : those of *H. muscinus* are less expanded with their width equal to four or five times their distance apart. The angular process of the mandible is elongate, connected to the articular process by a thin web of bone. This condition is very evident in *H. semoni*, which in this respect exactly resembles the series studied by Tate as represented by these specimens : it is much less pronounced in *H. muscinus.* The anterior upper premolar (pm²) is minute, extruded from the toothrow, with the canine and the second upper premolar (pm⁴) in contact : this is the condition exhibited by *H. semoni* and not by *H. muscinus* in which the anterior upper premolar is larger and separates the canine and the second upper premolar. The posterior ridge of the third upper molar is nearly as long as the anterior ridge, the W-pattern of the tooth almost complete, as in *H. semoni* and *H. stenotis :* in *H. muscinus* the posterior ridge is less than one third the length of the anterior ridge and the W-pattern of the tooth is incomplete.

These specimens must be referred to *H. semoni* and agree exactly with A.M.N.H. 154710, a female from Upper Nesbit River, Cape York, Queensland (labelled *Hipposideros muscinus semoni*), with B.M. 99.10.24.1, a female, also from Queensland and with B.M. 50.1154–1155, a male and female from the Buntibasa district, Kratke Mountains, Northeast New Guinea. The collections of the British Museum (Natural History) also contain a specimen from Avera, Aroa River, Papua, B.M. 4.4.11.4, with only the rostrum and mandible remaining of the skull, which must be referred to this species. Tate, who thus studied *H. semoni* in the mistaken belief that he had before him specimens of *H. muscinus,* thus came to the logical conclusion that *H. muscinus* and *H. semoni* were conspecific. Furthermore, he wrote (1941 : 379) " Dahl and Collett, both of whom wrote in 1897, evidently had North Australian material, which they alluded to as *muscinus* ". However, at that time neither *H. semoni* nor *H. stenotis* had been described, and Tate was apparently unaware that one of the specimens collected by Dahl at the Mary River, Northern Territory, Australia and referred by Dahl (1897 : 191) and Collett (1897 : 320) to *H. muscinus* was received by the British Museum (Natural History) in exchange with the then Christiania Museum in 1897 and subsequently became the type specimen of *H. stenotis.*

For the present, *H. semoni* and *H. stenotis* are treated as distinct species, although their differences are those of degree rather than of structure. *Hipposideros stenotis,* however, is a much smaller bat than *H. semoni,* and has the protuberances of the intermediate leaf and especially the posterior leaf less greatly developed. The frontal depression is more greatly excavated than in *H. semoni* and its rostral eminences are less inflated, while its anteorbital foramen is larger in relation to the size of its skull. The teeth of *H. stenotis* are smaller and less massive than those of *H. semoni.* The anterior upper premolar (pm²) in *H. stenotis* is absent : in *H. semoni* this tooth is absent in the type (Thomas (1913b : 206)) but is present in both sides of the jaw of all the specimens of *H. semoni* examined during the preparation of these notes.

Relationships within the group are summarized in Figure 19. The *muscinus* group evidently originates from within the *bicolor* group or from the *bicolor-speoris* stem and some of its features are incipiently displayed by *H. papua,* a species remotely allied to *H. bicolor* and its allies. The *muscinus* group is isolated within *Hipposideros* by the highly modified characters of its ears, noseleaves and auditory region, which are specialized to an extent otherwise nowhere approached in this large genus. Its extremely discontinuous distribution and the complexity of its characters suggest a relict group of remote origin, a view supported by the profound differences between its Ethiopian representatives and its remaining representatives in the Australasian region.

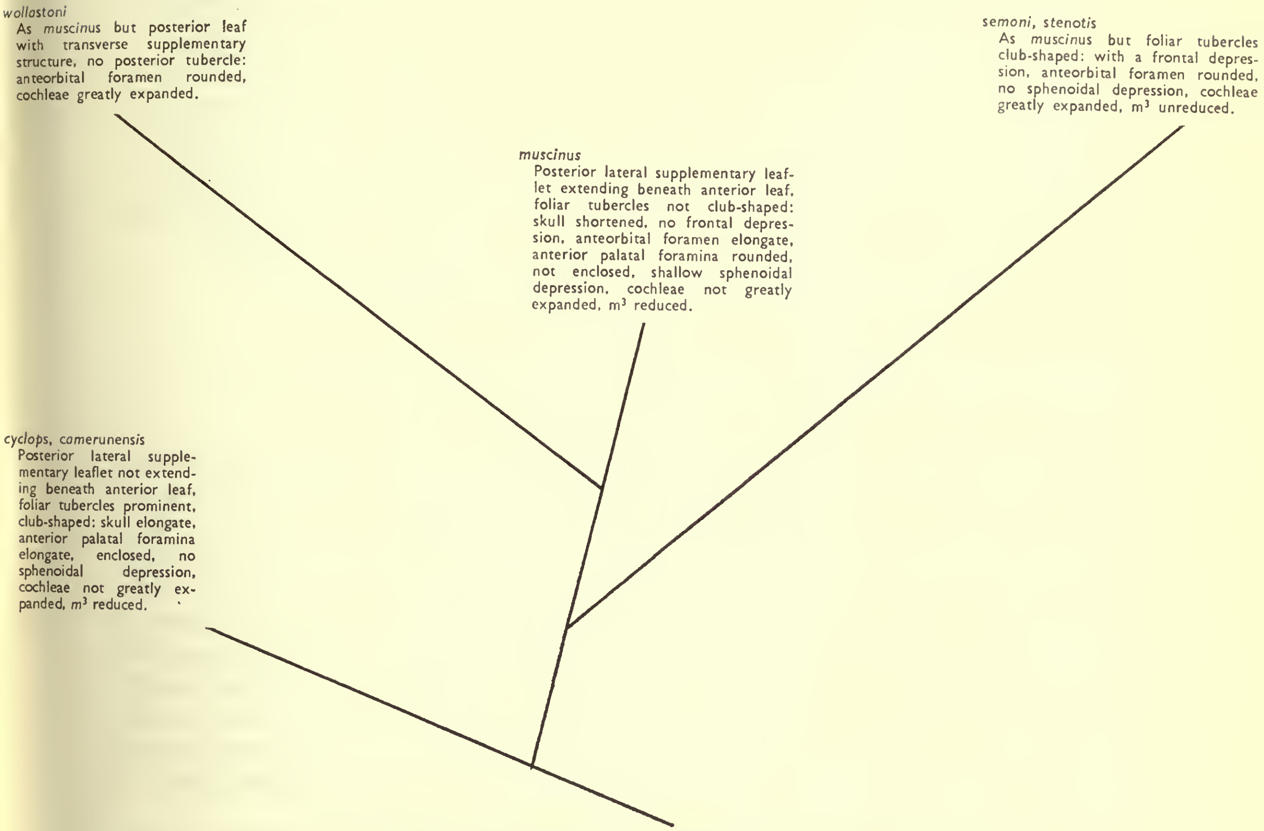

wollastoni
As *muscinus* but posterior leaf with transverse supplementary structure, no posterior tubercle: anteorbital foramen rounded, cochleae greatly expanded.
semoni, stenotis
As *muscinus* but foliar tubercles club-shaped: with a frontal depression, anteorbital foramen rounded, no sphenoidal depression, cochleae greatly expanded, m³ unreduced.
muscinus
Posterior lateral supplementary leaflet extending beneath anterior leaf, foliar tubercles not club-shaped: skull shortened, no frontal depression, anteorbital foramen elongate, anterior palatal foramina rounded, not enclosed, shallow sphenoidal depression, cochleae not greatly expanded, m³ reduced.
cyclops, camerunensis
Posterior lateral supplementary leaflet not extending beneath anterior leaf, foliar tubercles prominent, club-shaped: skull elongate, anterior palatal foramina elongate, enclosed, no sphenoidal depression, cochleae not greatly expanded, *m*³ reduced.

Fig. 19. Possible relationships in the *Hipposideros muscinus* group

The species of the *cyclops* group may be keyed :

1 Posterior lateral supplementary leaflet not extending anteriorly beneath the anterior leaf : premaxillae wide, enclosing the anterior palatal foramina, making a broad junction with the maxillae 2

Posterior lateral supplementary leaflet extending anteriorly beneath the anterior leaf : premaxillae narrow, not enclosing the anterior palatal foramina, making a narrow, spatulate junction with the maxillae 3

2 Smaller, length of forearm less than 74·0 mm.: anteorbital foramen relatively large *cyclops* (p. 78)

Larger, length of forearm exceeding 74·0 mm.: anteorbital foramen relatively small *camerunensis* (p. 80)

3 Median process of intermediate leaf not greatly developed or club-shaped : frontal depression absent, shallow sphenoidal depression present, posterior ridge of m³ reduced, W-pattern of tooth incomplete 4

Median process of intermediate leaf well developed, club-shaped : frontal depression present, sphenoidal depression absent, posterior ridge of m^3 little reduced, W-pattern of tooth almost complete 5

4 Posterior leaf with a median process and without a transverse supplementary structure developed from its posterior face : width of cochleae four to five times their distance apart . . . . *muscinus* (p. 81)

Posterior leaf without a median process and with a transverse supplementary structure developed from its posterior face : width of cochleae six or more times their distance apart . . . . *wollastoni* (p. 83)

5 Median process of posterior leaf well developed : frontal depression shallow, rostral eminences greatly inflated, anteorbital foramen relatively small . . *semoni* (p. 84)

Median process of posterior leaf not greatly developed : frontal depression deep, rostral eminences moderately inflated, anteorbital foramen relatively large . . *stenotis* (p. 86)

Hipposideros cyclops (Temminck)

(Figure 20)

Phyllorrhina cyclops Temminck, 1853 : 75. River Boutry, Ghana.
Rhinolophus micaceus De Winton, 1897 : 524. Como River, 75 miles from Gaboon.
Hipposideros langi J. A. Allen, 1917 : 434. Avakubi, eastern Congo.

The ears are exceptionally long and narrow, their posterior margins with a concavity behind the tip and without antitragal modification. The noseleaf is large, with two lateral supplementary leaflets. The anterior leaflet is short but wide : the posterior leaflet extends upwards to join the base of the posterior leaf but does not extend anteriorly beneath the anterior leaf. The anterior leaf has no median emargination, the internarial septum is not greatly inflated and the narial lappets are slightly expanded. The intermediate part of the leaf is flat but is specialized by the development of a median club-like process. The posterior leaf is moderately high, its upper edge more or less semicircular, thickened but not lobulated, and is supported by three septa enclosing deep pockets. It is specialized by the development of a median club-like process from the upper part of its anterior face. A frontal sac is present in both sexes.

The skull is large and elongate, with an elongate braincase and low sagittal crest. The interorbital region is rather constricted but not greatly shortened, and the supraorbital ridges are well defined. There is a moderate frontal depression and the rostral eminences are moderately inflated, separated by a shallow groove. The zygomata are comparatively massive, with a low jugal projection. The anteorbital foramen is large and rounded, closed by a moderate bar of bone. The premaxillae are broad, together almost filling the anterior palatal emargination, and wholly enclose the anterior palatal foramina. They are very wide posteriorly and make a broad, shallowly V-shaped junction with the maxillae. The palate is short, with a square palation. The mesopterygoid fossa is moderate, with the vomer projecting very slightly, and the pterygoids are long, with the sphenoidal bridge only very slightly constricted, almost completely concealing narrow, elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are large, their width equal to four times their distance apart. The upper incisors are

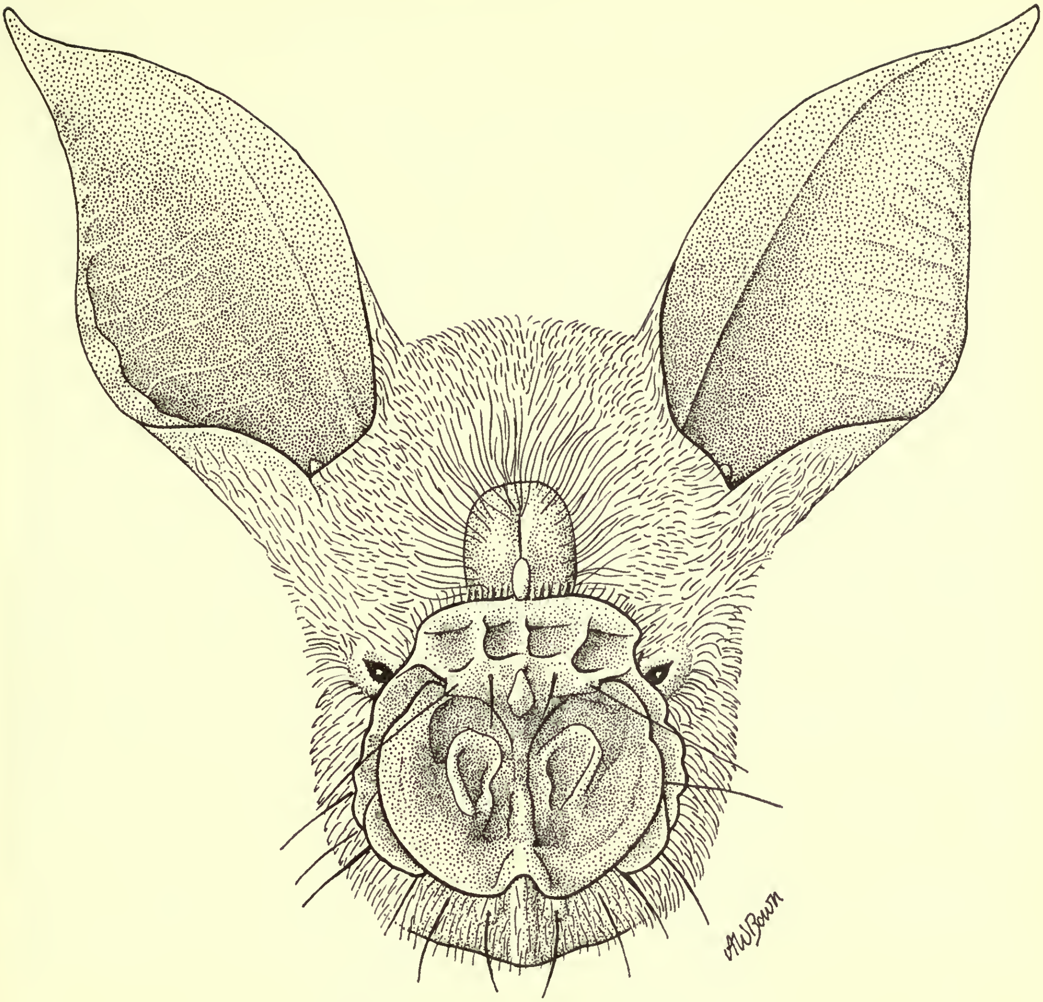


FIG. 20. *Hipposideros cyclops* ♂ (B.M. 30.11.11.151) (x3)

very weakly bilobed, and the upper canines lack cusps but have prominent cingula. The anterior upper premolar (pm^2) is not greatly reduced but is extruded from the toothrow with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is one third the length of the anterior ridge. The crown area of the outer lower incisors is equal to or slightly exceeds the crown area of the inner pair and the anterior lower premolar (pm_2) is much reduced, one quarter the length and one half the height of the second lower premolar (pm_4). Hayman (1935) gives an account of *H. cyclops*.

DISTRIBUTION : Portuguese Guinea (Veiga Ferreira (1949 : 195)) ; Sierra Leone ; Liberia ; Ghana ; Nigeria ; Cameroons ; Congo ; Kenya ; Uganda.

Hipposideros camerunensis Eisentraut

Hipposideros camerunensis Eisentraut, 1956 : 526. Buea, Cameroons.

The ears and noseleaf of *H. camerunensis* closely resemble those of *H. cyclops* but the ears of *H. camerunensis* are rather larger and the noseleaf is broader than in this species. A frontal sac is present in both sexes. The skull is similar to that of *H. cyclops* and is long and rather elongate, with a broadened braincase and low sagittal crest. The interorbital region is sharply constricted with well-defined supraorbital ridges. There is a moderate frontal depression and the rostrum is expanded and broad, with moderately inflated rostral eminences separated by a shallow groove. The zygomata are massive, with a moderate jugal projection. The anteorbital foramen is comparatively small, closed by a narrow bar of bone. The premaxillae are broad, like those of *H. cyclops*, together almost filling the anterior palatal emargination, and wholly enclose the elongate anterior palatal foramina. As in *H. cyclops*, they are wide posteriorly, and make a broad, shallowly V-shaped junction with the maxillae. The palate is short and the palation almost square. The mesopterygoid fossa is moderate, the vomer projecting very slightly, and the pterygoids are long with the sphenoidal bridge only slightly constricted and almost concealing elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are large as in *H. cyclops*, their width equal to four times their distance apart. The dentition almost exactly resembles that of *H. cyclops*. The upper incisors are weakly bilobed, the upper canines lack cusps and the anterior upper premolar (pm^2) is not greatly reduced, extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is one third the length of the anterior ridge. The crown area of the outer lower incisors slightly exceeds the crown area of the inner pair and the anterior lower premolar (pm_2) is one quarter the length and one half or slightly less the height of the second lower premolar (pm_4).

Hipposideros camerunensis is closely related to *H. cyclops* and differs from this species in its larger size, broader skull with broader braincase and rostrum and

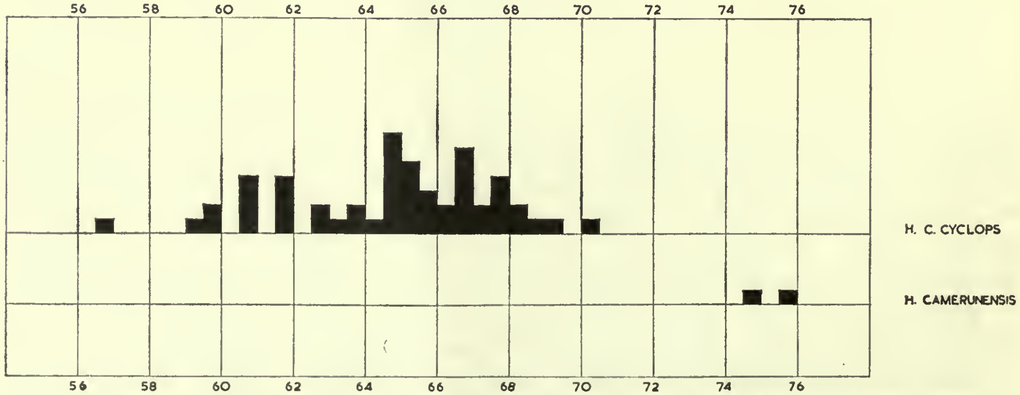


FIG. 21. Length of forearm in *Hipposideros cyclops* and *H. camerunensis*

smaller anteorbital foramen. The two species are the most primitive of the *cyclops* group, with their skulls elongate and not markedly shortened as in *H. muscinus* and its allies. Nevertheless, they display the specializations of the group to a considerable degree, notably in the elongation of their ears, the development of foliar prominences and the enlargement of their cochleae. Eisentraut (1963 : 87) discusses the status of *H. camerunensis* and records further specimens from Buea, Cameroons.

DISTRIBUTION : Cameroons ; Congo (first record : specimen from Shabunda, eastern Congo, in collection of British Museum (Natural History)).

Hipposideros muscinus (Thomas & Doria)
(Figure 22)

Phyllorrhina muscina Thomas & Doria, 1886 : 201, 1 fig. Fly River, Papua.

The ears are very long and comparatively narrow, although not excessively so, with their posterior margins slightly concave behind the tip. They lack any antitragal modification and are largely naked. The noseleaf is large, with two lateral supplementary leaflets. The anterior leaflet is short and broad, projecting widely beyond the lateral margin of the anterior leaf. The posterior leaflet is broad and extends posteriorly to join the posterior leaf and anteriorly beneath the anterior leaf on to the upper lip. The anterior leaf has no median emargination and the internarial septum is slightly swollen, especially anteriorly. The narial lappets are well developed, but the nostrils are only slightly pocketed. The intermediate part of the leaf is very slightly inflated with a small median tubercle-like process. The posterior leaf is high, its upper edge flattened, thickened and with a small median

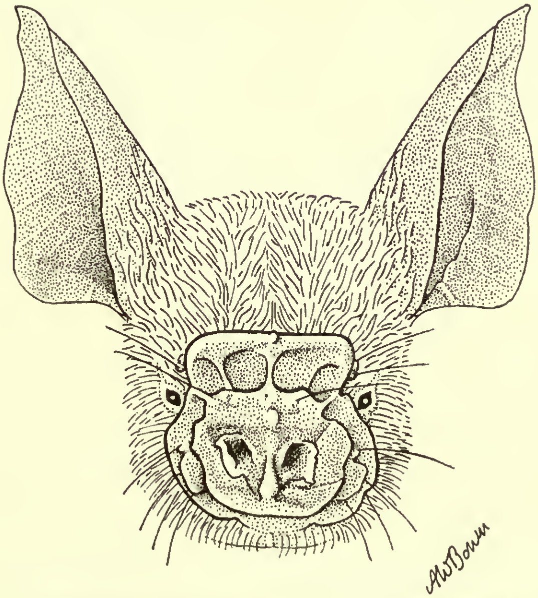


FIG. 22. *Hipposideros muscinus* ♀ (Syntype B.M. 86.11.3.10) (x3)

projecting tubercle. The posterior leaf is supported by three septa enclosing shallow pockets.

The skull is small, short and broad, with a low sagittal crest. The interorbital region is short and sharply constricted, the supraorbital ridges well defined. There is no frontal depression and the rostral eminences are moderately inflated, separated by a shallow groove. The zygomata are slender, with a low jugal projection and the anteorbital foramen is small, elongate and closed by a narrow bar. The junction of the premaxillae with the palate is U-shaped : the palate is very short with a U-shaped palation. The mesopterygoid fossa is wide, the pterygoids long and wide and the sphenoidal bridge barely constricted, partially concealing elongate lateral apertures. There is a shallow sphenoidal depression bisected by a low median ridge. The cochleae are large, their width equal to four or five times their distance apart. The upper canines are slender, without cusps, and the anterior upper premolar (pm^2) is not excessively reduced and is only slightly out of alignment in the toothrow, separating the canine and the second upper premolar (pm^4). The posterior ridge of the third upper molar is obsolescent, its length less than one quarter the length of the anterior ridge. The crown area of the outer lower incisors is slightly greater than the crown area of the inner pair and the anterior lower premolar (pm_2) is one third the length and height of the second lower premolar (pm_4).

Although the only specimen available for study is the syntype, there is no reason to consider that *H. muscinus* is conspecific with either *H. semoni* or *H. stenotis*. *Hipposideros muscinus* has ears shorter and broader than in these species, and has the projecting processes of the intermediate and posterior noseleaves less developed. Cranially, it differs quite markedly from either, with more sharply defined supraorbital ridges and a wider rostrum, the rostral eminences less inflated, the rostrum from its lateral aspect horizontal above, lacking the marked concavity over the interorbital region separating the rostral eminences and braincase in *H. semoni* and *H. stenotis* and lacking the frontal depression found in these species. In *H. muscinus* the anteorbital foramen is small and elongate, in contrast to the rounded foramina of *H. semoni* and *H. stenotis* : the sphenoidal bridge of *H. muscinus* is wider than in these species and a sphenoidal depression, absent in both, is present in *H. muscinus*. Its cochleae are less expanded than those of *H. semoni* or *H. stenotis* and the angular and articular processes of the mandible are not markedly connected by a thin web of bone as in these species. The third upper molar of *H. muscinus* has its posterior ridge greatly reduced and almost obsolete, contrary to the condition evident in *H. semoni* and *H. stenotis*, which have the posterior ridge of this tooth nearly equal in length to the anterior ridge and almost entire. These considerations indicate that while *H. muscinus* without doubt is allied to *H. semoni* and *H. stenotis*, it can by no means be considered conspecific with either of these species. It is less specialized than either *H. semoni* or *H. stenotis*, and cranially is similar to *H. wollastoni*. This species, however, differs from *H. muscinus* in the development of a transverse supplementary structure from the posterior face of the posterior leaf, in more inflated rostral eminences (similar in fact to those of *H. semoni* and *H. stenotis*) and in a greater degree of expansion of the cochleae.

Hipposideros wollastoni Thomas

Hipposideros wollastoni Thomas, 1913b : 205. Camp 3, Utakwa River, southwestern Netherlands New Guinea.

The ears are long and comparatively narrow, pointed, their posterior margins slightly concave behind the tip. They lack antitragal modification and are largely naked. The noseleaf is large with two lateral supplementary leaflets exactly similar to those of *H. muscinus*. The anterior leaf resembles that of *H. muscinus* but the internarial septum is slightly more inflated and the nostrils are slightly pocketed. The intermediate leaf is not inflated but has a large projecting median eminence. The upper edge of the intermediate part of the leaf is elevated laterally, these elevations forming a base for and largely concealing the lateral supporting septa of the posterior leaf. The posterior leaf has its upper edge semicircular, unthickened and lacking a median projection, and is supported by three septa enclosing shallow pockets. A transverse supplementary structure with a serrate upper edge is developed from its posterior face, and is equal in height almost to the posterior leaf. This structure is joined longitudinally to the posterior leaf by two external and two intermediate septa, enclosing three small pockets. A wart-like eminence arises on each side of the muzzle just behind the posterior leaf. There is a small depression but no frontal sac in the female type specimen.

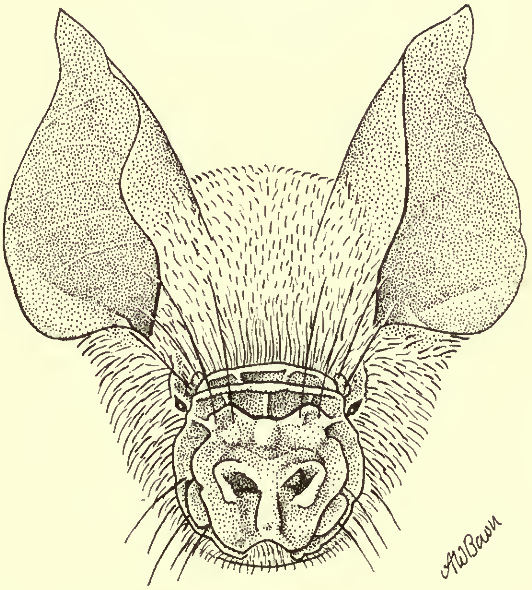


FIG. 23. *Hipposideros wollastoni* ♀ (Type B.M. 13.6.18.4) (x3)

The skull in general outline is very like that of *H. muscinus*, with a moderate sagittal crest and a constricted interorbital region. The supraorbital ridges are evident but not sharply defined, especially behind the rostral eminences. There is no frontal depression and the rostral eminences are considerably inflated, separated by a deep groove, and give the rostrum from its lateral aspect a marked elevation. The zygomata are slender, with a moderate jugal projection while the anteorbital foramen is small, rather rounded and closed by a narrow bar. The premaxillae are narrow, spatulate posteriorly, and make a narrow junction with the maxillae. They do not enclose the rounded anterior palatal foramina, the anterior walls of which are formed by the delicate anterior enclosing processes of the premaxillae. The palate is short and the palation U-shaped with a small post-palatal spicule. The mesopterygoid fossa is wide and the pterygoids are long, with an almost unconstricted sphenoidal bridge, partially concealing elongate lateral apertures. There is a small sphenoidal depression, lacking any median ridge. The cochleae are greatly expanded, their width equal to six times their distance apart. The angular and articular processes of the mandible are not markedly connected by a web of bone. The upper incisors are not bilobed and the upper canines lack cusps, while the anterior upper premolar (pm^2) is small and extruded, the canine and the second upper premolar (pm^4) almost in contact. The posterior ridge of the third upper molar is equal in length to one third of the length of the anterior ridge, the W-pattern of the tooth incomplete. The crown area of the outer lower incisors is slightly greater than that of the inner pair, and the anterior lower premolar (pm_2) is a little under one half the length and height of the second lower premolar (pm_4).

Despite its specialized noseleaf, *H. wollastoni* is more closely related to *H. muscinus* than to *H. semoni* or *H. stenotis*. Its ears, which are more acutely pointed than those of *H. muscinus* but shorter and broader than those of *H. semoni* or *H. stenotis*, its more advanced noseleaf, broader, more inflated rostrum and more greatly expanded cochleae show *H. wollastoni* to be a more specialized bat than *H. muscinus*.

Hipposideros semoni Matschie

(Figure 24)

Hipposideros semoni Matschie, 1903 : 774 (Heft 6 : 132). Cooktown, northern Queensland.

The ears are very long and narrow, with an acute, narrow point. Their posterior margins are markedly concave just behind the tip, they lack any antitragal modification and are haired for one third of their length. The noseleaf is a highly developed structure covering much of the muzzle, and has two lateral supplementary leaflets. The anterior leaflet is short and broad, projecting widely beyond the lateral margin of the anterior leaf as in *H. muscinus* and *H. wollastoni*. As in these species, the posterior leaflet extends posteriorly to become continuous with the posterior leaf and anteriorly beneath the anterior leaf. The anterior leaf has no median emargination and the internarial septum is slightly inflated with the narial lappets well developed, the nostrils not pocketed. The intermediate part of the leaf is flat, its upper edge elevated laterally and bears a very well-developed club-shaped projection. The posterior leaf is high, supported by three septa, its upper edge semicircular, with a well-developed median club-shaped projection.

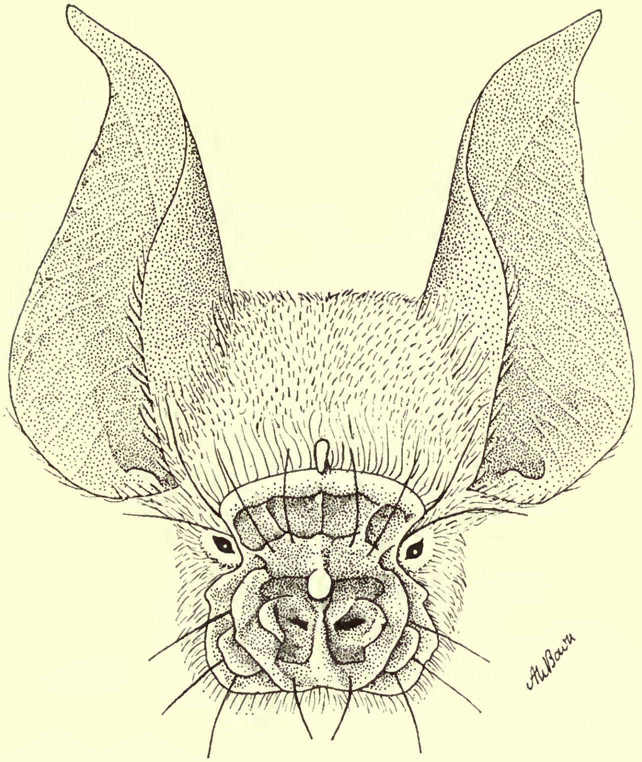


Fig. 24. *Hipposideros semoni* ♀ (B.M. 99.10.24.1) (x3)

The skull is short and broad, with a broad braincase and prominent sagittal crest. The interorbital region is moderately constricted with prominent supraorbital ridges which are less developed behind the rostral eminences. There is a shallow frontal depression and the rostral eminences are greatly inflated, to give the rostrum from its lateral aspect a much elevated appearance, deeply concave above the interorbital region. The zygomata are moderate, with a low jugal process and the anteorbital foramen is small and round, separated by a narrow bar. The premaxillae are much as in *H. wollastoni*, narrow, spatulate posteriorly and making a narrow junction with the maxillae. They do not enclose the rounded anterior palatal foramina. The palate is short, the palation square with a post-palatal spicule. The mesopterygoid fossa is wide while the pterygoids are long and the sphenoidal bridge moderately constricted, exposing elongate lateral apertures. There is no sphenoidal depression, but the sphenoidal region is traversed by a low longitudinal ridge. The cochleae are enormous, their width equal to eight times their distance apart, almost touching, separated by a very narrow basioccipital. The angular and articular processes of the mandible are united by a thin web of bone. The upper incisors are weakly bilobed, the upper canines without cusps and the anterior upper premolar (pm^2) very small, extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact : Thomas (1913b : 206) notes that this tooth is absent in the type specimen. The posterior ridge of the third upper molar is not greatly reduced, its length equal to two thirds the length of the anterior ridge and with the W-pattern of the tooth almost complete. The crown area of the outer lower incisors is slightly greater than that of the inner pair and the anterior lower premolar (pm_2) is less than one quarter the length and height of the second lower premolar (pm_4).

Hipposideros semoni is clearly quite distinct from *H. muscinus*, differing from this species in a number of salient features, among which the greater development of the ears and noseleaf, rostrum and cochleae are the most important. It is patently one of the most, if not the most specialized species of the *cyclops* group and together with the closely related *H. stenotis* represents the culmination of a line of specialization of which *H. papua* is perhaps an offshoot and *H. muscinus* a later development.

Distribution : Northern Australia ; Papua ; Northeast New Guinea.

Hipposideros stenotis Thomas
(Figure 25)

Hipposideros stenotis Thomas, 1913b : 206. Mary River, Northern Territory, Australia.

Externally, *H. stenotis* is closely similar to *H. semoni* but is considerably smaller. The ears are exactly as described for that species, while the noseleaf almost exactly resembles that of *H. semoni* except that the median projection of the posterior leaf is less prominent. The skull is short and broad, with moderate sagittal crest and supraorbital ridges like those of *H. semoni*. There is a deep frontal depression and the rostral eminences are moderately inflated, sufficiently that the rostrum from its lateral aspect appears elevated. The zygomata are slender, with a low jugal projection and the anteorbital foramen is rounded, closed by a narrow bar. The premaxillae are similar to those of *H. wollastoni* and *H. semoni*, spatulate posteriorly, making a narrow junction with the maxillae and not enclosing the rounded anterior palatal foramina. The palate is short and the palation square, with a small post-palatal spicule. The mesopterygoid fossa is moderate, the pterygoids long and the sphenoidal bridge moderately constricted exposing wide, elongated lateral apertures. There is no sphenoidal depression and the sphenoidal region is traversed by a low longitudinal ridge. The cochleae are enormous, their width equal to eight times their distance apart, almost touching, separated by a very narrow basioccipital. The angular and articular processes of the mandible are connected by a web of bone. The upper incisors are weak and not bilobed : the type specimen is unusual in that a second right hand upper incisor is present. It is a peg-like tooth, longer but more slender than the first upper incisor. The upper canines lack cusps and the anterior upper premolar (pm^2) is absent, with the canine and the second upper premolar (pm^4) in contact. The posterior ridge of the third upper molar is not greatly reduced and is two thirds the length of the anterior ridge, with the W-pattern of the tooth almost complete. The crown area of the outer lower incisors is a little greater than that of the inner pair and the anterior lower premolar (pm_2) is much reduced, one quarter the length and height of the second lower premolar (pm_4).

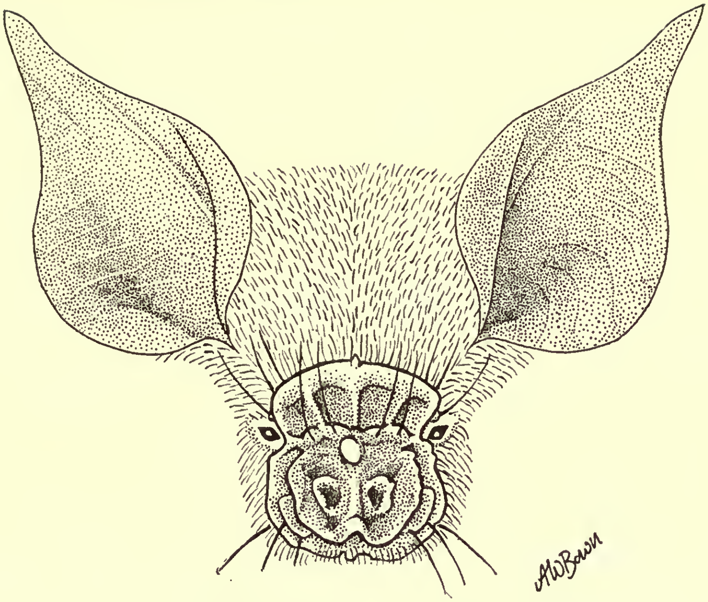


FIG. 25. *Hipposideros stenotis* ♀ (Type B.M. 97.4.12.7) (x3)

Although the close structural similarity of *H. stenotis* to *H. semoni* suggests that the two may be conspecific, there is considerable disparity in size and *H. stenotis* has the protuberances of its intermediate and posterior noseleaves less developed. Cranially, its frontal depression is deeper than that of *H. semoni* and its rostral eminences less inflated : its anteorbital foramen is larger and the molars much less massive. Only the type specimen of *H. stenotis* is available for study and for the present it is retained as a distinct species. Tate (1941 : 389) records a series of *H. stenotis* from Papua in the collections of the American Museum of Natural History. Despite careful search by the authorities of that Museum, no trace of this series has been found.

HIPPOSIDEROS PRATTI group

This group contains only two species, *H. pratti* and *H. lylei*, both Asiatic in distribution. The ears are large and broad, bluntly pointed with their posterior margins slightly concave behind the tip. They lack antitragal modification and are haired for one third of their length. The noseleaf has two lateral supplementary leaflets and the anterior leaf a median emargination. The intermediate part of the leaf is expanded, with a median eminence and the posterior leaf is high in the centre, triangular, supported by a prominent median ridge flanked by two much weaker ridges. The group is noteworthy for the development of transverse fleshy lobate prominences on each side of the opening of the frontal sac to form a structure resembling a supplementary posterior noseleaf traversing the muzzle behind the true posterior leaf. The degree of development of this structure varies considerably, but is always at its greatest in male specimens.

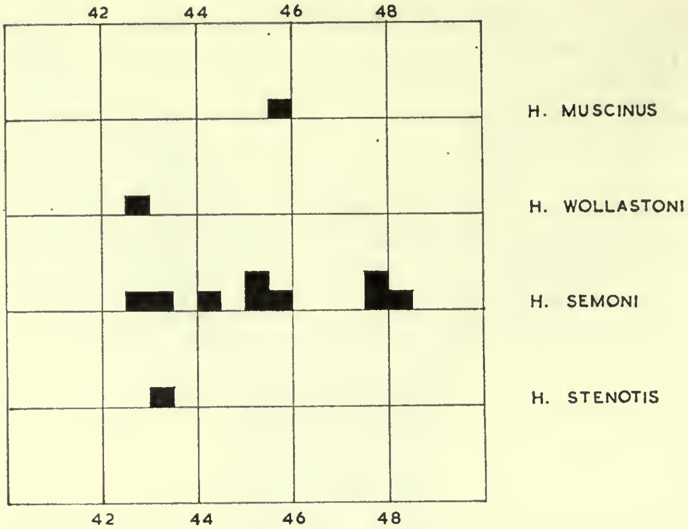


FIG. 26. Length of forearm in *Hipposideros muscinus*, *H. wollastoni*, *H. semoni* and *H. stenotis*

The skull is of moderate to large size, with a moderate sagittal crest. The interorbital region is short, with well-defined supraorbital ridges and there is a shallow frontal depression. The rostrum is low and broad with moderately inflated rostral eminences. The zygomata are slender and have a moderate jugal projection, while the anteorbital foramen is rounded and closed by a narrow bar. The premaxillae make a fan-shaped junction with the maxillae and totally enclose the rounded anterior palatal foramina. The palate is short and wide, the pterygoids comparatively short and the sphenoidal bridge not markedly constricted. There is a well-defined sphenoidal depression and the cochleae are small, their width equal to or less than their distance apart. The outer lobe of the upper incisors is only slightly smaller than the inner lobe, and the anterior upper premolar (pm^2) is reduced, extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is almost obsolete. The crown area of the outer lower incisors is greater than that of the inner pair, and the anterior lower premolar is one half the length and height of the second lower premolar (pm_4).

Although Ellerman & Morrison-Scott (1951 : 129) considered *H. pratti* and *H. lylei* to be conspecific, the two evidently are widely separated by differences in the structure of the noseleaf and cranial architecture which in no way support the view that they are conspecific. Their taxonomic position within the genus is not easy to determine. The presence of two lateral supplementary leaflets and their short, broadened skulls recalls the more specialized species of the *bicolor* group while the development of a supplementary lobate structure behind the posterior leaf in both forms and the presence of an abrupt discontinuity between the roofs of the mesopterygoid and narial canals in *H. pratti* suggest an affinity with the *armiger* group.

The depressed rostrum and the presence of a frontal depression in the *pratti* group, however, render close alliance with the *armiger* group unlikely. In the present work, the *pratti* group is regarded as linking bats of the *bicolor* group to the more specialized bats of the *armiger* group, displaying no affinities towards either the *speoris* or *diadema* groups.

The two species of the *pratti* group may be keyed :

1 Lateral margins of anterior leaf not continuous with those of posterior leaf : rostrum lacking lateral pits, an abrupt step-like discontinuity between roofs of narial and mesopterygoid canals, vomer projecting posteriorly beyond palate . *pratti* (p. 89)
Lateral margins of anterior and posterior leaves continuous : rostrum with lateral pits, roofs of narial and mesopterygoid canals merging smoothly, vomer not projecting posteriorly beyond palate . . . . . . *lylei* (p. 90)

Hipposideros pratti Thomas

Hipposiderus (sic) *pratti* Thomas, 1891 : 527. Kiatingfu, Szechuan, China.

The ears and noseleaf agree closely with the group description. The anterior leaf has a single median emargination and its lateral margins are not continuous with those of the posterior leaf. The internarial septum is uninflated and the narial lappets moderately developed. The intermediate part of the leaf is inflated with a prominent median eminence. Its upper edge is elevated laterally to form a large transverse structure across the noseleaf anterior to the lower part of the posterior leaf. The posterior leaf is more or less triangular in outline and is supported by a well-defined median septum, flanked laterally by weaker ridges, barely enclosing small cells. Two large lobate projections are developed transversely behind the posterior leaf, one each side of the opening of the frontal sac, to form an enlarged supplementary transverse structure, the projections separated by a deep median notch at the aperture of the sac. A small tuft of bristle-like hairs projects through this notch. This transverse structure is more greatly developed in old male animals than in young male or female examples. A frontal sac is present in both sexes.

The skull is large and broad, with a well-developed sagittal crest. The interorbital region is markedly constricted and there are prominent supraorbital ridges. There is a shallow frontal depression and the rostrum is broad, its upper surface below the level of that of the braincase, bluntly angular, with a pentagonal outline and with the rostral eminences not greatly inflated. The zygomata and the anteorbital foramen are as described for the group as are the premaxillae, which make a U-shaped junction with the maxillae. The palation is U-shaped and the mesopterygoid fossa wide with the posterior part of the narial canal deeply excavated, an abrupt step-like discontinuity separating its roof from the roof of the mesopterygoid fossa. The vomer is thin and blade-like, projecting posteriorly beyond the edge of the palate. The pterygoids are moderate and the sphenoidal bridge constricted, exposing wide, elongate apertures. The sphenoidal depression, cochleae and dentition are as described for the group. Osgood (1932 : 222) gives detailed illustrated notes on specimens from Tonkin.

Pohle (1943 : 323) considers a specimen in the Berlin Museum to be the holotype of *Phyllorhina swinhoii* Peters (in Swinhoe, Proc. zool. Soc. Lond. 1870 (1871) : 616) (more correctly *swinhoei*) and has suggested that *H. pratti* is synonymous with the species described by Peters. However, Peters (1871a : 317) considered *H. swinhoei* to be a synonym of *H. armiger* (Hodgson) and was followed in this opinion by Dobson (1878 : 135) and Andersen (1906a : 37) while Tate (1941 : 371, 389) who had available a photograph " of the type skull ", a topotype from Amoy and other specimens from China, considered *H. swinhoei* to be a subspecies of *H. armiger*. There are three specimens from the original series collected by Swinhoe in the collections of the British Museum (Natural History). All have three lateral supplementary leaflets and cannot therefore be regarded as *H. pratti*. In the present work *H. swinhoei* (Peters) is regarded as a synonym of *H. armiger armiger* (Hodgson).

DISTRIBUTION : Southwestern China ; Indochina : Tonkin.

Hipposideros lylei Thomas

Hipposideros lylei Thomas, 1913a : 88. Chiendao Cave, 50 miles north of Chiengmai, Siam, 350 metres.

The ears are broad and triangular, slightly less acutely pointed than in *H. pratti*, their posterior margins shallowly concave behind the tip and slightly thickened at the antitragal lobe. The noseleaf in its essentials resembles that of *H. pratti*, with two small lateral supplementary leaflets, but is slightly more specialized. The anterior leaf projects forward over the upper lip and has a deep median emargination, the edge of the leaf lateral to this emargination shallowly emarginated on each side to form two small projecting lappets. Its lateral margins are continuous with those of the posterior leaf but are separated from them at the level of the intermediate part of the leaf by a shallow notch on each side. The internarial septum is not greatly inflated and the narial lappets are well developed. The intermediate part of the leaf is similar to that of *H. pratti* and has a well-developed median eminence. Its lateral margins are embellished on each side with a small outwardly projecting lappet at the level of the notches in the lateral margins of the anterior and posterior leaves. The posterior leaf is triangular in outline and is supported by a median septum and two weaker lateral ridges. There is a greatly developed transverse supplementary structure behind the posterior leaf as described for *H. pratti*.

The skull is of moderate to large size, with a low sagittal crest. The interorbital region is markedly constricted and the interorbital ridges are sharply defined. There is a well-developed frontal depression and the rostrum is broad, low as in *H. pratti*, with the rostral eminences slightly inflated. There is a lateral depression on each side of the rostrum immediately above the anteorbital foramen : these depressions are a little deeper than the frontal depression. The zygomata are moderate with a moderate jugal process and the anteorbital foramen, premaxillae and palate are as described for the group, the premaxillae making a broad, U-shaped junction with the maxillae and the palation more acute, almost V-shaped. The mesopterygoid fossa is wide, and the roof of the narial canal, although discontinuous with the roof of the mesopterygoid canal, merges into it smoothly, without an abrupt, step-like discontinuity. The vomer does not project posteriorly beyond the edge of the palate. The pterygoids are short and wide, the sphenoidal bridge less constricted than in *H. pratti*, partially concealing elongate lateral apertures. The sphenoidal depression, cochleae and dentition are as described for the group.

Hipposideros lylei differs from *H. pratti* in the deeper median emargination of its anterior leaf, flanked by two shallow lateral emarginations absent in *H. pratti :* in the continuity of the lateral margins of the anterior and posterior noseleaves, which are separated only by lateral marginal notches and in the presence of small lateral lappets at the margins of the intermediate part of the leaf. It has a deeper frontal depression : lateral rostral pits, present in *H. lylei*, are absent in *H. pratti* and the zygomata of *H. lylei* are more massive than those of *H. pratti*. In *H. lylei* the roofs of the narial and mesopterygoid canals merge smoothly, without the abrupt, step-like discontinuity characteristic of *H. pratti* and the sphenoidal bridge of *H. lylei* is wider than that of *H. pratti*, partially concealing the lateral apertures.

DISTRIBUTION : Burma ; North Shan States ; Siam ; Federation of Malaya.

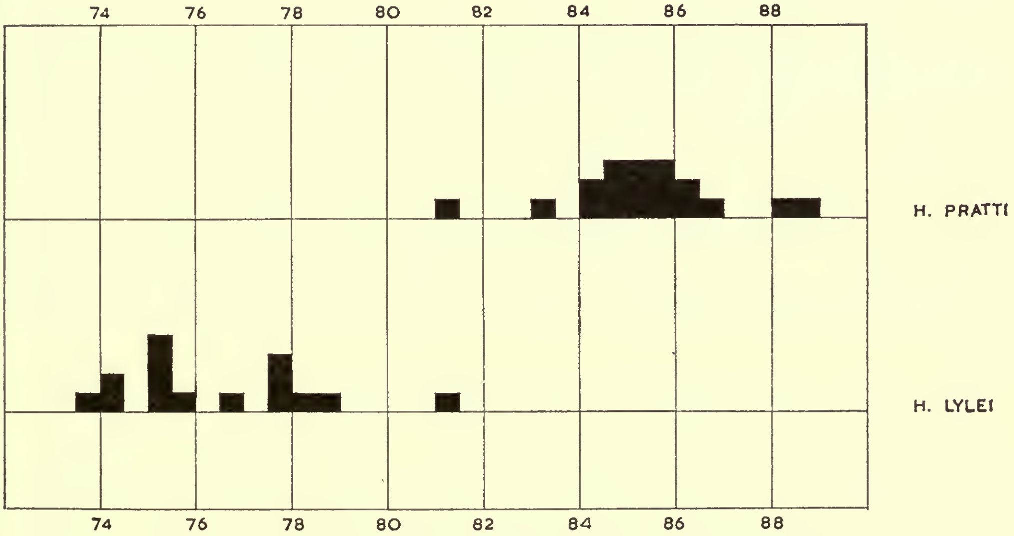


FIG. 27. Length of forearm in *Hipposideros pratti* and *H. lylei*

HIPPOSIDEROS ARMIGER group

The ears are large, broad and acutely pointed, their posterior margins concave behind the tip. They are slightly thickened at the antitragal lobe and are haired for one third of their length. The noseleaf is broad, with four supplementary leaflets, the fourth small, sometimes rudimentary. The anterior leaf has no distinct median notch, the internarial septum is not inflated and the narial lappets are not greatly developed. The intermediate part of the leaf is slightly inflated with a prominent median eminence. The posterior leaf is high and narrow, not as wide as the anterior leaf, its upper edge flattened, thickened, becoming trilobate and is supported by a prominent median septum and two less evident lateral septa. Prominent fleshy elevations arise behind the posterior leaf on each side above the eyes to form a transverse supplementary structure, found at its greatest development in old male specimens, less developed in young male and female examples. There is a frontal sac in male specimens : in female examples it is small or is represented by a depression.

The skull is of moderate to large size with well-developed sagittal crest, short, constricted interorbital region and sharply defined supraorbital ridges. There is no frontal depression and the rostral eminences are uninflated. The naso-frontal region is decidedly pentagonal in outline and the rostrum is elevated posteriorly, in profile forming a nearly horizontal surface on a level with the upper surface of the braincase. The zygomata are moderate to strong, with a moderate to well-developed jugal projection. The anteorbital foramen is large and rounded, closed by a very narrow bar. The premaxillae make a fan-shaped junction with the maxillae and do not enclose the elongate anterior palatal foramina. The palation is U-shaped and the mesopterygoid fossa wide, with the roof of the narial canal separated from the roof of the mesopterygoid fossa by a sharp, step-like discontinuity, the vomer projecting beyond the edge of the palate. The pterygoid wings are expanded and the sphenoidal bridge is wide, almost concealing elongate lateral apertures. There is a moderate sphenoidal depression and the cochleae are small, their width less than their distance apart. The upper incisors are bilobed with the outer lobe approximately equal to the inner lobe while the upper canines have a low anterior cusp. The anterior upper premolar (pm^2) is small, extruded from the toothrow with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is greater than that of the inner pair and the anterior lower premolar (pm_2) is one third to one half the length and height of the second lower premolar (pm_4).

The *armiger* group contains two very closely related species, *H. armiger* and *H. turpis*, essentially identical in their structural characteristics and separable only by the much smaller size of *H. turpis* as compared with *H. armiger*, a situation not unparalleled elsewhere in *Hipposideros*. The group is a specialized one not closely related to the other group of large bats of the genus *Hipposideros*, the *diadema* group, with which it was compared by Andersen (1906a : 35). Its affinities lie with the *pratti* group with which the *armiger* group shares a number of specializations in the development of lobate transverse structures behind the posterior noseleaf, broad premaxillae joined to the maxillae by a wide, fan-shaped junction, a sharp discontinuity between the roofs of the narial and mesopterygoid canals (least developed in *H. lylei*, more so in *H. pratti*, *H. armiger* and *H. turpis*) and small cochleae. The *armiger* group, although having the transverse lobes behind the noseleaf less developed than in the *pratti* group, seems nevertheless slightly more specialized with a shorter, less elongate skull, no frontal depression, a high rostrum level with the upper surface of the braincase and with the canine-bearing parts of the maxillae not prolonged anteriorly. The *armiger* group seems to have developed from the *speoris-diadema* stem, to which it is linked by the *pratti* group.

Hipposideros armiger

Size large, otherwise characters as in the group diagnosis.

DISTRIBUTION : Northern India to Formosa and the Malay Peninsula.

Hipposideros armiger armiger (Hodgson)

Rhinolophus armiger Hodgson, 1835 : 699. Nepal.
Phyllorhina swinhoii Peters, 1871b : 616. Amoy, Fukien.
Hipposideros armiger debilis Andersen, 1906a : 37. Province Wellesley, Federation of Malaya.

The status of *Phyllorhina swinhoii* Peters has been discussed in connection with *H. pratti*. The diagnosis of *H. a. debilis* Andersen rests entirely on a slightly narrower interorbital region and shorter mandibular toothrow in Malayan specimens when compared with *H. a. armiger*. Long series in the collections of the British Museum (Natural History) do not support this contention.

DISTRIBUTION : Northern India ; Nepal ; Assam ; Burma ; southern China ; Hong Kong (Romer (1960 : 2)) ; Indochina : Tonkin (Osgood (1932 : 222)), Bourret (1942b : 11)) ; Federation of Malaya ; Langkawi Island.

Hipposideros armiger terasensis Kishida

Hipposideros armiger terasensis Kishida, 1924 : 42. Formosa.

According to Tate (1941 : 390) *H. a. terasensis* is likely to prove indistinguishable from *H. a. armiger*.

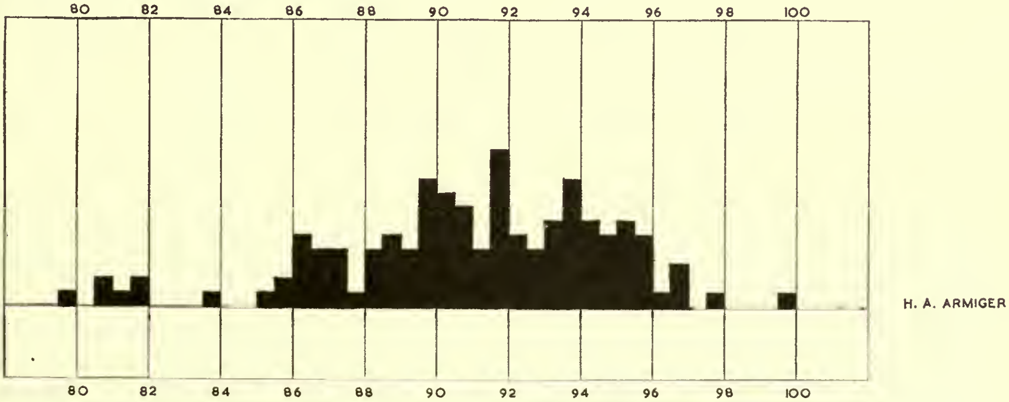


FIG. 28. Length of forearm in *Hipposideros armiger*

Hipposideros armiger tranninhensis Bourret

Hipposideros tranninhensis Bourret, 1942a : 20. Plaine des Jarres, Tran-Ninh, Indochina.

From the description (repeated in part by Bourret (1942b : 12)) this form appears to be a subspecies of *H. armiger*, distinguished from *H. a. armiger* by its more trilobate posterior noseleaf.

Hipposideros turpis

The characters of this species are exactly as in *H. armiger* but it is, however, of much smaller size. The two species of the *armiger* group provide a close parallel to the situation found in some other groups of *Hipposideros* whereby two closely similar species differing chiefly in size are found to be sympatric. Such is the case with *H. galeritus* and *H. breviceps ; H. caffer* and *H. beatus ; H. cyclops* and *H. camerunensis ; H. lankadiva* and *H. schistaceus* and also *H. diadema* and *H. dinops*. In all of these, however, there is a small degree of structural differentiation between each pair of species : *H. armiger* and *H. turpis* are exceptional in that they differ only in size.

Hipposideros turpis turpis Bangs

Hipposideros turpis Bangs, 1901 : 561. Ishigaki, South Liukiu Islands.

Hipposideros turpis pendleburyi Chasen

Hipposideros pendleburyi Chasen, 1936 : 133. Near the foot of Khao Ram, Nakon Sri Tamarat, Peninsular Siam.

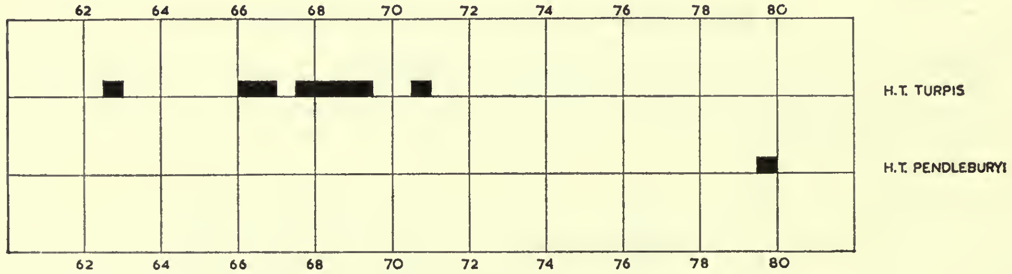
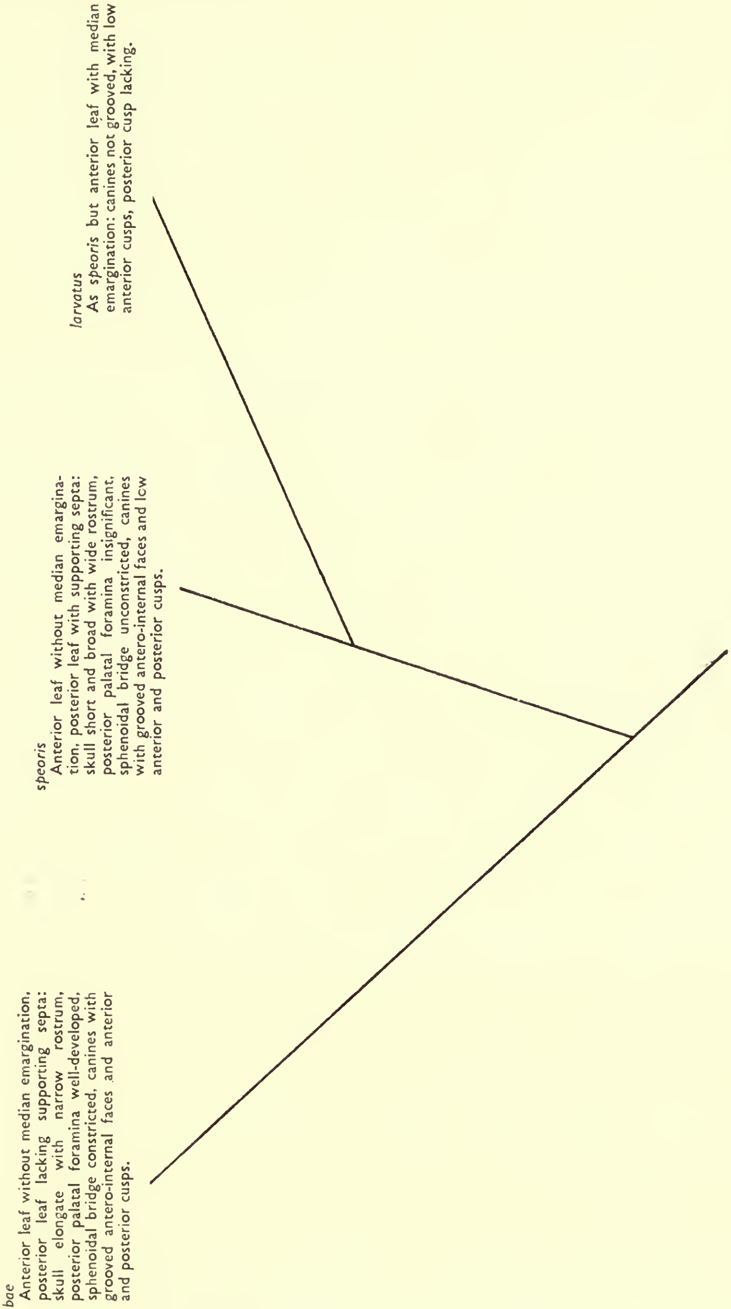


Fig. 29. Length of forearm in *Hipposideros turpis*

HIPPOSIDEROS SPEORIS group

The ears are large and comparatively broad, triangular in outline, their posterior margins concave behind the tip. Either there is a small process at the antitragal lobe or the membrane of the ear is thickened at this point. The noseleaf is simple, with three lateral supplementary leaflets. The skull is of medium size, comparatively short and with a moderate sagittal crest. The interorbital region is short and constricted and the supraorbital ridges are well developed. There is no definite frontal depression and the rostrum is low, with moderately inflated rostral eminences.

The zygomata are slender with a moderate jugal projection and the anteorbital foramen is rounded and closed by a narrow bar. The premaxillae make a wedge-



abae
Anterior leaf without median emargination, posterior leaf lacking supporting septa: skull elongate with narrow rostrum, posterior palatal foramina well-developed, sphenoidal bridge constricted, canines with grooved antero-internal faces and anterior and posterior cusps.

speoris
Anterior leaf without median emargination, posterior leaf with supporting septa: skull short and broad with wide rostrum, posterior palatal foramina insignificant, sphenoidal bridge unconstricted, canines with grooved antero-internal faces and low anterior and posterior cusps.

larvatus
As *speoris* but anterior leaf with median emargination: canines not grooved, with low anterior cusps, posterior cusp lacking.

FIG. 30. Possible relationships in the *Hipposideros speoris* group

shaped or slightly U-shaped junction with the maxillae and partially or wholly enclose the anterior palatal foramina. The palate is short and wide with a V-shaped or U-shaped palation. The pterygoid wings are not greatly developed and the sphenoidal bridge is not widened, exposing elongate lateral apertures. There is a well-developed sphenoidal depression and the width of the cochleae is equal to their distance apart. The outer lobe of the upper incisors is obsolescent or absent and the upper canines have no definite cusps, although barely defined low anterior and posterior cusps are sometimes present. The anterior upper premolar (pm^2) is small and extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is obsolete or nearly obsolete. The outer lower incisors are greater in crown area than the inner pair and the anterior lower premolar (pm$_2$) is one half to two thirds the length and height of the second lower premolar (pm$_4$).

As presently defined, the *speoris* group includes three species, *H. abae*, *H. larvatus* and *H. speoris*. It is distributed in both the Ethiopian and Asiatic regions, with *H. abae* representing the group in Africa while *H. larvatus* and *H. speoris* are exclusively Asiatic in distribution. As might be expected, *H. abae* is rather sharply divided from the Asiatic species to much the same degree as the Ethiopian representatives of the *bicolor* group are from their Asiatic relatives, although its affinities lie nearer to the predominantly Indian species *H. speoris* than to the more Malaysian *H. larvatus*. The group is not one of extensive specialization in the manner of some of the members of the *bicolor* or *cyclops* groups and in fact the ears of its members retain some degree of antitragal modification and their nasal foliations are comparatively simple, apart from the development of a third lateral supplementary leaflet. The structure of the ears and noseleaves in the *speoris* group indicates quite clearly its affinity to the *bicolor* group, and similar indications are evident in its cranial architecture, although specialization has proceeded further. In the *speoris* group the anterior palatal foramina in *H. larvatus* are wholly enclosed within the premaxillae and in the other species partially so ; the upper canine cusps are virtually obsolete and the crown area of the outer lower incisors is greater than the crown area of the inner pair. The *speoris* group apparently represents an offshoot of the line leading to the *diadema* group and has no close relation to the *pratti* and *armiger* groups, which represent a different line of modification characterized by the marked development of noseleaves, rostral region and mesopterygoidal region.

The species of the *speoris* group may be keyed :

1 Anterior leaf without median emargination : prominent supraorbital ridges, rostrum flattened, vomer not projecting beyond palate, upper canines with shallow antero-internal groove and low posterior cusp 2

Anterior leaf with definite median emargination: supraorbital ridges barely developed, rostrum rounded, vomer projecting beyond palate, upper canines not grooved and lacking a posterior cusp . . . . *larvatus* (p. 98)

2 Posterior leaf with supporting septa : posterior palatal foramina undeveloped, palation U-shaped, sphenoidal bridge unconstricted . . . . *speoris* (p. 101)

Posterior leaf lacking supporting septa : posterior palatal foramina prominent, palation nearly square, sphenoidal bridge constricted . . . *abae* (p. 97)

Hipposideros abae J. A. Allen

Hipposideros abae J. A. Allen, 1917 : 432. Aba, Uele district, Congo.

The ears are very large, triangular and sharply pointed, with their posterior margins markedly concave behind the tip. There is no definite process at the antitragal lobe, but the ear membrane is thickened at this point. The anterior leaf has no median emargination and the internarial septum is not inflated, while the narial lappets are moderately developed. The intermediate part of the leaf is not greatly inflated and has a low median eminence flanked by weaker lateral eminences. The posterior leaf is thin and lacks supporting septa, with its upper edge semicircular and not lobate. The skull is slightly more elongate than the skull of *H. speoris*, with a low to moderate sagittal crest. The interorbital region is elongate and constricted with prominent supraorbital ridges. There is a very shallow frontal depression and the rostrum is narrow, with slightly inflated rostral eminences. The zygomata are slender anteriorly, with a high jugal process, and the anteorbital foramen is large and elongate, closed by a narrow bar. The premaxillae make a slightly wedge-shaped junction with the palate and partially or wholly enclose the elongate anterior palatal foramina. The posterior palatal foramina, small and insignificant in *H. larvatus* and *H. speoris*, are well developed and the palation is almost square. The mesopterygoid fossa is wide, with the vomer not projecting beyond the posterior edge of the palate and with expanded pterygoids. The sphenoidal bridge is narrow and sharply constricted, exposing large elongate lateral apertures. There is a well-developed sphenoidal depression and the cochleae are equal in width to their distance apart or are a little smaller. The upper incisors are large, weakly bilobed and situated near the outer corners of the premaxillae, while the upper canines have their anterior faces shallowly grooved and have a weak anterior cusp and a larger posterior cusp extending for one quarter of the height of the tooth. The anterior upper premolar (pm^2) is small, extruded, compressed between the canine and the second upper premolar (pm^4) with these teeth nearly in contact, while the posterior ridge of the third upper molar is one quarter or less the length of the anterior ridge. The crown area of the outer lower incisors is only slightly greater than that of the inner pair, and the anterior lower premolar (pm_2) is one half or slightly less the length and height of the second lower premolar (pm_4).

Hipposideros abae is divided sharply from *H. larvatus* and *H. speoris* by both external and cranial characters. It is a larger species, with the posterior leaf lacking supporting septa. Its interorbital region is more elongated than in the Asiatic species, its rostrum narrower with the anterior part of the maxillae bearing the canines more elongated, and it has a much larger anteorbital foramen. The premaxillae are broader and its prominent posterior palatal foramina, nearly square palation and constricted sphenoidal bridge are in direct contrast to the insignificant foramina, U-shaped palations and unconstricted sphenoidal bridges of *H. larvatus* and *H. speoris*. Such differences indicate comparatively remote divergence from the Asiatic members of the group and although in some respects such as its elongate skull and narrow, elongate rostrum *H. abae* is more primitive than *H. larvatus* or

H. speoris, it has the grooved upper canines of *H. speoris* and at the same time has developed independent specializations in its unsupported posterior leaf, prominent posterior palatal foramina and constricted sphenoidal region. The position of *H. abae* within the group is difficult to determine in view of these considerations. Its elongate skull and narrow rostrum suggest some affinity with the *bicolor* group and *H. abae* evidently forms a link between that group and the *speoris* group, but it is otherwise as specialized as *H. larvatus* and *H. speoris* in some features and in others perhaps more so. The degree of affinity of *H. abae* to its Asiatic relatives is similar to that of *H. jonesi* to its related Asiatic species in the *bicolor* group or to that of *H. cyclops* and *H. camerunensis* to the related Australian and Papuan species of the *cyclops* group. *Hipposideros abae*, however, is rather less divergent from its associated Asiatic species than *H. jonesi*, *H. cyclops* and *H. camerunensis* are from their closest congeners in the Asiatic and Australasian regions, perhaps reflecting a slightly less remote dichotomy in the *speoris* group. Its degree of divergence from its Asiatic relatives is paralleled by *H. caffer* and its associated species, which have a similar affinity to the Asiatic *H. galeritus* and its allies, while the African *H. commersoni* diverges less from the related Asiatic *H. diadema* than *H. abae* does from *H. larvatus* and *H. speoris*.

DISTRIBUTION : Portuguese Guinea (Veiga Ferreira (1949 : 192)) ; Guinea (Aellen (1956a : 888), Eisentraut & Knorr (1957 : 331)) ; Sierra Leone ; Ghana ; Nigeria ; Congo ; Uganda (first record : specimen from Metu, West Madi County, West Nile District, in collection of British Museum (Natural History)).

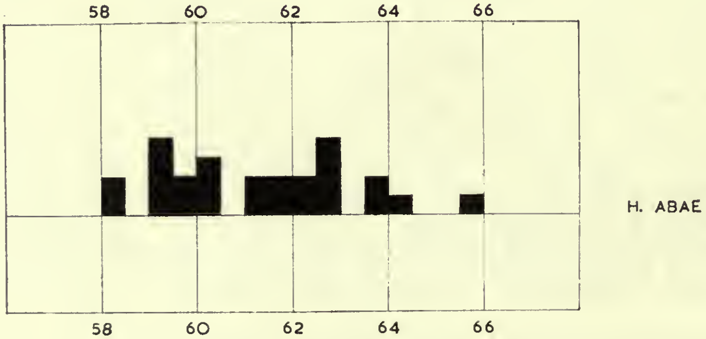


FIG. 31. Length of forearm in *Hipposideros abae*

Hipposideros larvatus

The ears are as described for the group, with a small process at the antitragal fold. The anterior leaf has a small but distinct median emargination, the internarial septum is uninflated and the narial lappets are well developed, the nostrils slightly pocketed. The intermediate part of the leaf is slightly expanded, with a moderate median eminence and weaker lateral eminences. The posterior leaf is moderate, supported by three well-defined septa, its upper edge semicircular but slightly flattened and thickened, displaying a tendency to become lobate. There is a frontal sac in both sexes, in females reduced sometimes to a depression containing a tuft of hairs. The skull is short and massive, with a well-developed sagittal crest and low supraorbital ridges. There is a shallow frontal depression and the rostral eminences are well inflated, separated by a shallow groove, the rostrum rounded. The anteorbital foramen is slightly elongate. The premaxillae make an acutely V-shaped junction with the maxillae and wholly enclose the slightly elongate anterior palatal foramina. The palation is U-shaped, with the vomer projecting beyond the posterior edge of the palate and the sphenoidal bridge only very slightly constricted, nearly parallel-sided. The sphenoidal depression is well developed. The upper incisors are weakly bilobed, the upper canines with a low anterior cusp but no posterior cusp and with their antero-internal faces not grooved. The anterior upper premolar (pm^2) is slightly extruded and compressed tightly between the canine and the second upper premolar (pm^4), while the posterior ridge of the third upper molar is one quarter the length of the anterior ridge. The anterior lower premolar (pm_2) is one third to one half the length of the second lower premolar (pm_4).

Although *H. larvatus* is very similar to *H. speoris*, the two species are separated by a number of differences indicating comparatively recent divergence. Of the two, *H. larvatus* is perhaps slightly the more primitive, with a prominent median emargination in the anterior leaf, longer interorbital region with less prominent supraorbital ridges, longer, rounded rostrum and ungrooved canines, although these have lost the posterior cusp. The two species are more closely related to each other than either is to the African species *H. abae*, which displays some affinities to *H. speoris* but clearly is widely separated from the two Asiatic species. *Hipposideros larvatus* exhibits a cline in size in southeast Asia : *H. l. grandis* from Burma and *H. l. alongensis* from Indochina are the largest subspecies, while *H. l. barbensis* from St. Barbe Island and *H. l. larvatus* from Java are the smallest. Specimens from Siam approach *H. l. grandis*, while those from Sumatra and its adjacent islands are nearer in size to *H. l. larvatus* : *H. l. neglectus* from Borneo and the Malay Peninsula is intermediate between these extremes.

DISTRIBUTION : Burma to Indochina and the Malay Peninsula ; Java ; Borneo ; Sumatra and adjacent islands.

Hipposideros larvatus larvatus (Horsfield)

Rhinolophus larvatus Horsfield, 1823 : No. 6, pl. Java.
Rhinolophus vulgaris Horsfield, 1823 : No. 6, pl. Java.
Rhinolophus deformis Horsfield, 1823 : No. 6, pl. Java.
Rhinolophus insignis Horsfield, 1823 : No. 6, pl. Java.

DISTRIBUTION : Java.

Hipposideros larvatus sumbae Oei

Hipposideros larvatus sumbae Oei, 1960 : 28. Eastern part of Sumba Island, Lesser Sunda Islands. Lectotype designated by Bree (1961 : 122).

Hipposideros larvatus barbensis Miller

Hipposideros barbensis Miller, 1900 : 233. St. Barbe Island, South China Sea.

DISTRIBUTION : St. Barbe Island ; Johore Archipelago : Aor Island (Hill (1960 : 28)).

Hipposideros larvatus neglectus Sody

Hipposideros larvatus neglectus Sody, 1936 : 46. Roema Manoeal, south foot of Mount Kenepai, central Indonesian Borneo.

Miller (1942 : 116) refers a specimen from Nias Island to *H. l. neglectus* but suggests that it may prove separable from both *H. l. larvatus* and *H. l. neglectus* : Hill (1960 : 28) provisionally refers specimens from Butang Island and Simalur Island to *H. l. neglectus*.

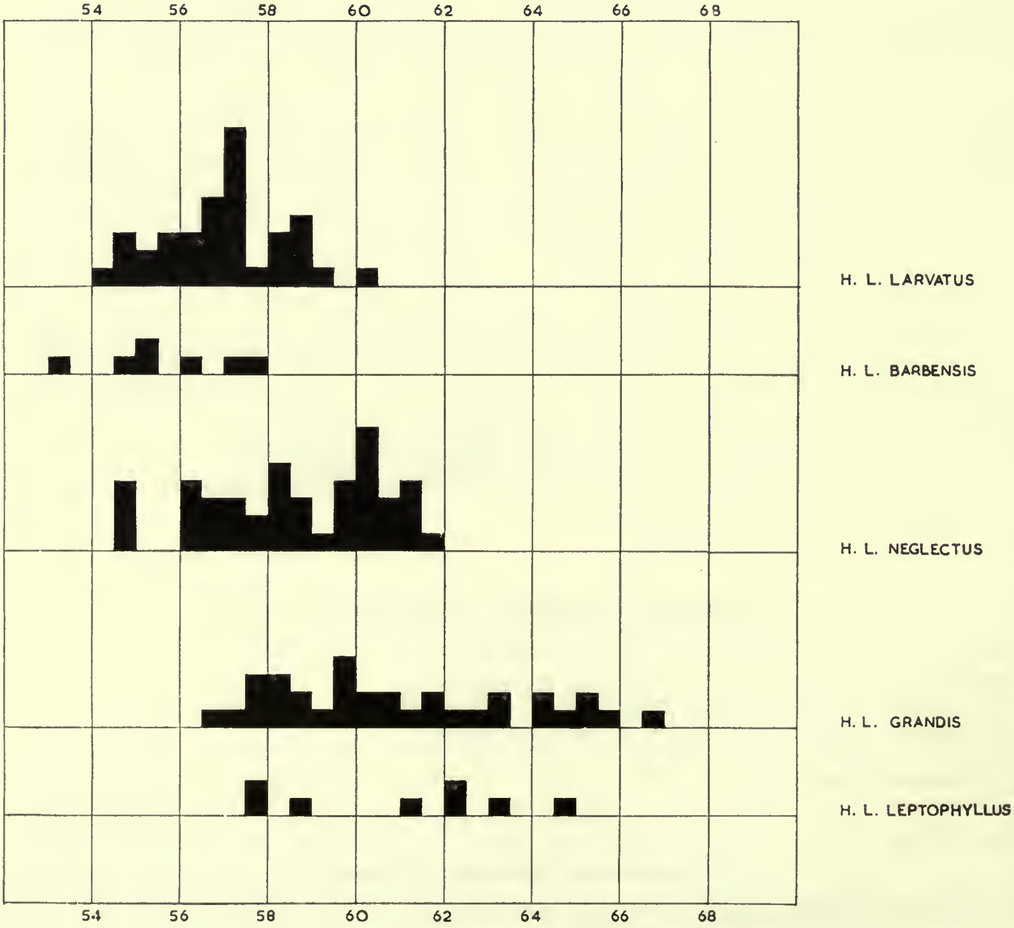


FIG. 32. Length of forearm in *Hipposideros larvatus*

Distribution : Borneo ; Karimata Island ; South Natuna Islands : Sirhassen Island ; Sumatra ; Nias Island ; Simalur Island ; Butang Island ; Malay Peninsula ; Tioman Island.

Hipposideros larvatus grandis G. M. Allen

Hipposideros larvatus grandis G. M. Allen, 1936 : 345. Akanti, Upper Chindwin, Burma, 500 feet.

Shamel (1942 : 322) compared *H. l. grandis* and *H. l. neglectus.*

Distribution : Burma ; Siam (Shamel (1942 : 322)) ; Indochina (part).

Hipposideros larvatus alongensis Bourret

Hipposideros larvatus alongensis Bourret, 1942a : 27. Bay d'Along, Indochina.

External measurements of a small series of specimens are given by Bourret (1942b : 10).

Hipposideros larvatus poutensis J. A. Allen

Hipposideros poutensis J. A. Allen, 1906 : 483. Pouten, Hainan.

Hipposideros larvatus leptophyllus (Dobson)

Phyllorhina leptophylla Dobson, 1874a : 234. Khasi Hills, Assam.

Hipposideros speoris

The ears are as described for the group, pointed, their posterior margins slightly concave behind the tip and have a small projecting process at the antitragal lobe. The anterior leaf has only a faint trace of a median emargination, the internarial septum is slightly inflated and the narial lappets are well developed, the nostrils slightly pocketed. The intermediate part of the leaf is slightly expanded, with inflated median and lateral eminences. The posterior leaf is supported by three septa and its upper edge is semicircular and not especially thickened. There is a frontal sac in male specimens : it is absent or represented by a tuft of hair in female examples. The skull is similar to the skull of *H. larvatus*, with a low to moderate sagittal crest and low but definite and more prominent supraorbital ridges. There is a shallow frontal depression and the rostral eminences are well inflated, the rostrum flattened dorsally. The premaxillae make an acutely angled wedge-shaped junction with the maxillae and partially or wholly enclose the rather elongate anterior palatal foramina. The palation is U-shaped and the vomer does not project beyond the edge of the palate. The sphenoidal bridge is moderate and only slightly constricted and there is a shallow but well-defined sphenoidal depression. The upper incisors are not bilobed or only very weakly so and the upper canines have low anterior and posterior cusps and a shallow groove on their antero-internal faces. The anterior upper premolar (pm^2) is slightly extruded, compressed tightly between the canine and the second upper premolar (pm^4), while the posterior ridge of the third upper molar is one third the length of the anterior ridge. The anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4). Brosset (1962 : 608) provides a study of the biology of *H. speoris* in India, with measurements and notes on its colour variation.

DISTRIBUTION : India ; Ceylon.

Hipposideros speoris speoris (Schneider)

Vespertilio speoris Schneider, 1800 : pl. 59b. Tate (1941 : 377) has suggested restriction of the type locality to Tranquebar, India : it is briefly reviewed by Oey & Feen (1958 : 231).
Rhinolophus marsupialis Desmarest, 1820 : 126.
Rhinolophus dukhunensis Sykes, 1831 : 99. Deccan, India.
Hipposideros apiculatus Gray, 1838 : 492. Madras, India.
Hipposideros templetonii Kelaart, 1850a : 208. Ceylon.
Hipposideros aureus Kelaart, 1853 : 18. Ceylon.
Hipposideros blythi Kelaart, 1853 : 20. Ceylon.

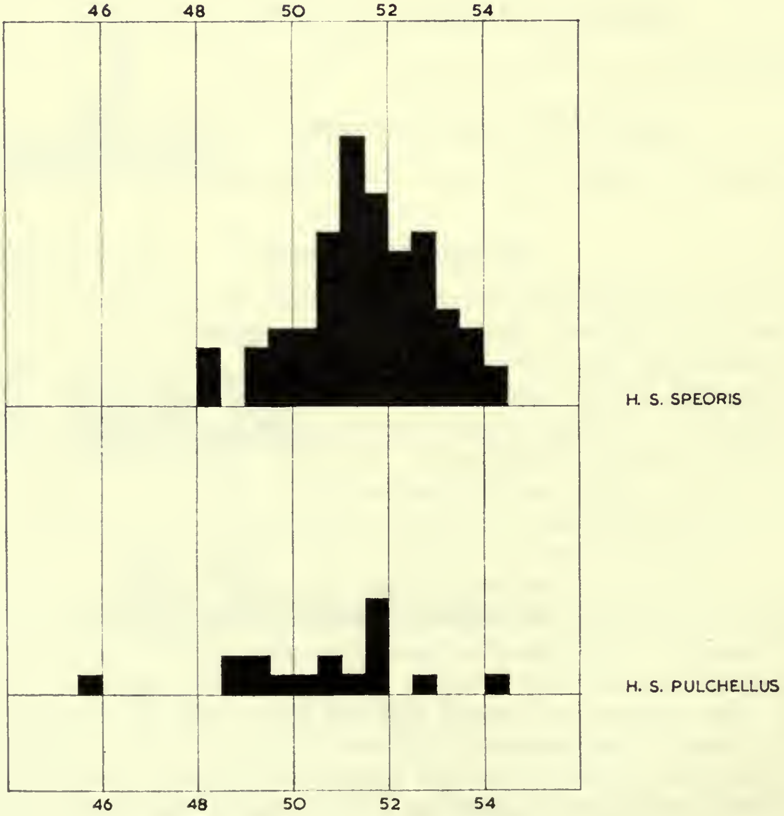


FIG. 33. Length of forearm in *Hipposideros speoris*

Oey & Feen (1958 : 227) discuss the date of description of *Vespertilio speoris* Schneider and reprint the original text. They also study (p. 232) the external differences between *H. speoris* and *H. larvatus* in considerable detail.

DISTRIBUTION : India (part) ; Ceylon.

Hipposideros speoris pulchellus Andersen

Hipposideros speoris pulchellus Andersen, 1918 : 383. Vijayanagar, Bellary, India.

DISTRIBUTION : India (part).

HIPPOSIDEROS DIADEMA group

The ears are triangular, acutely pointed, their posterior margins concave behind the tip, with no antitragal modifications. The noseleaf is comparatively simple, with three or four lateral supplementary leaflets. The anterior leaf has no median emargination and the internarial septum is not inflated. The intermediate part of the leaf is expanded and the posterior leaf is high, supported by a median septum and two weaker lateral septa. A frontal sac may be present or absent. The skull is large, with moderate or strongly developed cranial crests. A frontal depression is present in the majority of species. The rostral eminences are moderately inflated, the rostrum broad and high, its rounded upper surface level with the roof of the braincase. The zygomata are massive, with a prominent jugal process and the anteorbital foramen is large, elongate and closed by a narrow bar. The premaxillae make a wedge-shaped junction with the maxillae and partially or wholly enclose the anterior palatal foramina. The palate is short, the vomer not projecting or projecting only very slightly beyond its posterior edge. The mesopterygoid fossa is wide, the pterygoid wings expanded, terminating in delicate processes. The sphenoidal bridge is wide, partially concealing elongate lateral apertures. The sphenoidal depression is moderately developed and the cochleae are large, their width as great or greater than their distance apart. The mandible is massive, with a deep symphysis and a high coronoid process : the angular process is sometimes flexed outwards. The upper incisors are bilobed, the upper canines with or without a posterior cusp. The anterior upper premolar (pm^2) is small, partially or wholly extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is much reduced and obsolescent. The crown area of the outer lower incisors is greater than that of the inner pair and the anterior lower premolar (pm_2) is from one third the length and height to one half or two thirds the length and height of the second lower premolar (pm_4).

As defined in the present paper, the *diadema* group has been extended to include the *commersoni* group as listed by Tate (1941 : 358), including solely the African species *H. commersoni*. There appears no good reason for the wide separation of this species from the *diadema* group since it shares with *H. diadema* and its associated species a number of features indicative of a common origin. Like *H. diadema* and its allies, it is characterized by its acute, triangular ears, simple noseleaf with three or four lateral supplementary leaflets and massive skull with greatly developed cranial crests. As might be expected, the African *H. commersoni* is rather sharply

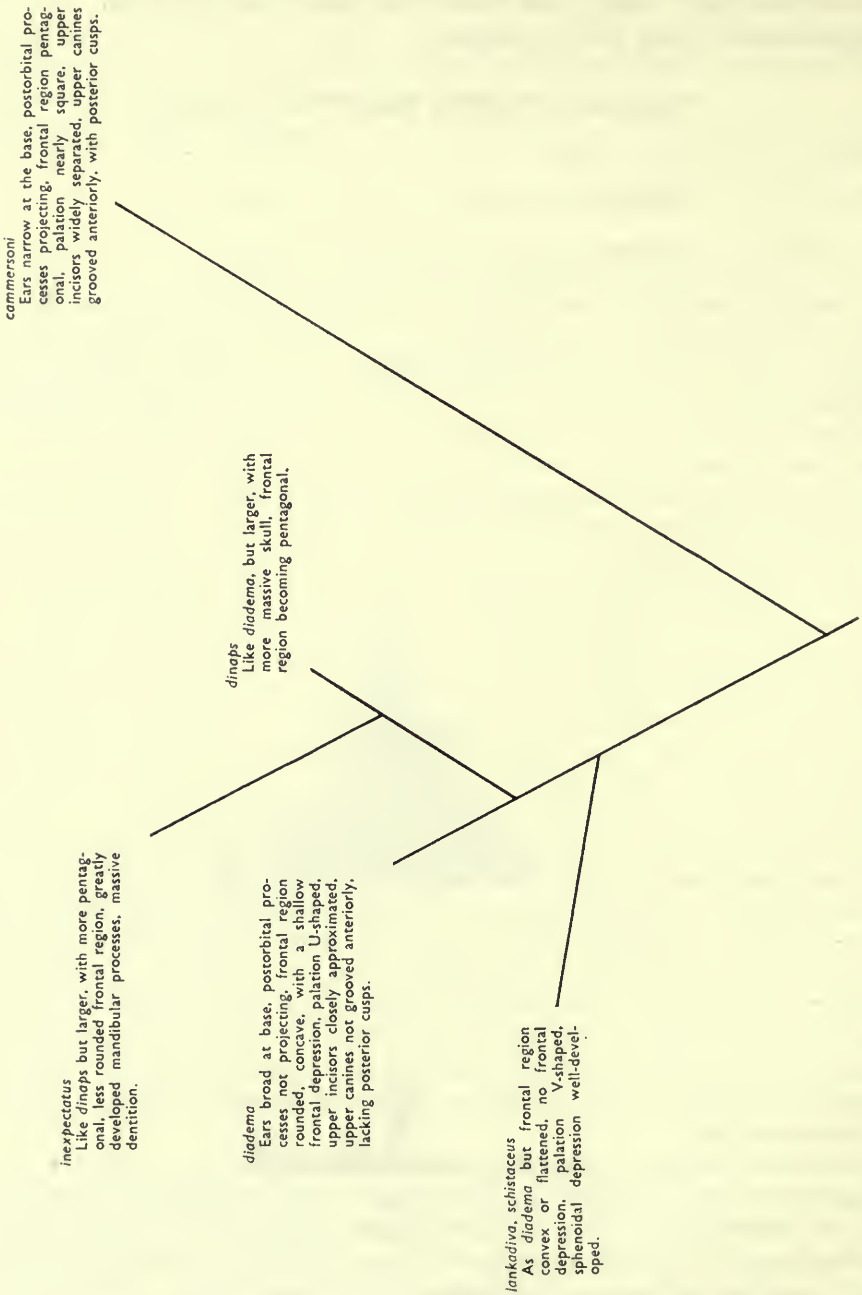

commersoni
Ears narrow at the base, postorbital processes projecting, frontal region pentagonal, palation nearly square, upper incisors widely separated, upper canines grooved anteriorly, with posterior cusps.
dinaps
Like *diadema*, but larger, with more massive skull, frontal region becoming pentagonal.
inexpectatus
Like *dinaps* but larger, with more pentagonal, less rounded frontal region, greatly developed mandibular processes, massive dentition.
diadema
Ears broad at base, postorbital processes not projecting, frontal region rounded, concave, with a shallow frontal depression, palation U-shaped, upper incisors closely approximated, upper canines not grooved anteriorly, lacking posterior cusps.
lankadiva, schistaceus
As *diadema* but frontal region convex or flattened, no frontal depression, palation V-shaped, sphenoidal depression well-developed.

FIG. 34. Possible relationships in the *Hipposideros diadema* group

separated from *H. diadema*, which with its allies forms a comparatively closely related group of wholly Asiatic and Australasian species. In general, these are more primitive and less modified than *H. commersoni*, with broader ears, less developed postorbital processes, the naso-frontal region rounded from its dorsal aspect and not pentagonal, and with the upper canines not grooved anteriorly. *Hipposideros lankadiva* and *H. schistaceus* are the least specialized species in the group : *H. diadema* and more particularly its immediate derivatives *H. dinops* and *H. inexpectatus* are more modified, while *H. commersoni* is the most advanced species of the group, with narrow ears, projecting postorbital processes, more pentagonal naso-frontal region, grooved canines and with the anterior premolars ($\mathrm{pm}\frac{2}{2}$) more reduced. Possible relationships of the species of the *diadema* group are summarized in Figure 34.

The species of the *diadema* group may be keyed :

1 Ears broad at base : postorbital processes not projecting, naso-frontal region rounded, upper incisors in contact or nearly so, upper canines not grooved anteriorly, lacking posterior cusps 2
Ears narrow at base : postorbital processes projecting, naso-frontal region pentagonal, upper incisors widely separated, upper canines grooved anteriorly, with high posterior cusp . . . . *commersoni* (.p 115)
2 Frontal region convex or flattened, no frontal depression ; palation acute, V-shaped ; sphenoidal depression well developed 3
Frontal region concave, with a shallow frontal depression ; palation rounded, U-shaped ; sphenoidal depression shallow 4
3 Skull larger, condylocanine length exceeding 26·5 mm., length of maxillary toothrow (c–m^3) exceeding 12·0 mm. . . . . *lankadiva* (p. 105)
Skull smaller, condylocanine length less than 25·5 mm., length of maxillary toothrow (c–m^3) less than 11·8 mm. . . . . *schistaceus* (p. 107)
4 Smaller, length of forearm less than 98·0 mm., condylocanine length less than 33·0 mm.; intermediate part of noseleaf with prominent median ridge, sometimes forming a projection 5
Larger, length of forearm exceeding 100 mm., condylocanine length exceeding 34·0 mm.; intermediate part of noseleaf swollen but without a prominent median ridge or projection . . . . *inexpectatus* (p. 113)
5 Smaller, length of forearm less than 92·0 mm., condylocanine length less than 31·0 mm., length of maxillary toothrow (c–m^3) less than 13·8 mm. . . *diadema* (p. 108)
Larger, length of forearm exceeding 92·0 mm., condylocanine length exceeding 32·0 mm., length of maxillary toothrow (c–m^3) exceeding 14·0 mm. *dinops* (p. 112)

Hipposideros lankadiva

The ears are large and acutely pointed, with their posterior margins slightly concave behind the tip. The noseleaf has usually four lateral supplementary leaflets, the fourth much reduced and rudimentary, sometimes absent. The anterior leaf has no median emargination and the internarial septum is not inflated, while the narial lappets are well developed. The intermediate part of the leaf is expanded, its central part inflated and swollen but not forming a distinct median ridge, flanked laterally by lesser eminences. The posterior leaf is high and broad, its upper margin semicircular, with a swollen median projection, flanked by narrow notches, and is supported by three well-defined septa enclosing small cells. The skull is large and heavily built, with well-developed cranial crests. There is no frontal depression and the frontal region immediately anterior to the sagittal crest is convex or flattened. The zygomata are strong, with a high jugal process, while the anteorbital foramen is large, elongate and closed by a narrow bar. The premaxillae make a U-shaped junction with the maxillae and enclose or nearly enclose the rounded anterior palatal foramina. The palation is V-shaped, the mesopterygoid fossa slightly narrowed with the vomer projecting slightly beyond the posterior edge of the palate. The sphenoidal bridge is wide, almost completely concealing elongate lateral apertures and the sphenoidal depression is well developed. The width of the cochleae is a little less than their distance apart. The mandible is massive, with a high coronoid process and the angular process flexed strongly outwards. The upper incisors are bilobed, the outer lobe a little larger than the inner lobe, and the upper canines are not grooved anteriorly : they have low anterior cusps but lack posterior cusps. The anterior upper premolar (pm^2) is small, extruded or partially extruded from the toothrow. The posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is considerably greater than that of the inner pair, and the anterior lower premolar (pm_2) is one third the length and height of the second lower premolar (pm_4).

Hipposideros lankadiva is closely related to *H. diadema* but is perhaps slightly less specialized. Externally, it is very similar to *H. diadema*, but the intermediate part of the noseleaf has no definite median ridge and the median projection of the edge of the posterior leaf is more swollen and prominent. Cranially, it differs rather sharply in its convex or flattened frontal region, which lacks the frontal depression of *H. diadema*, in its V-shaped and not U-shaped palation and in its well-developed sphenoidal depression. With the very closely related *H. schistaceus* it represents *H. diadema* in the Indian subcontinent. Brosset (1962 : 621) has studied the biology of *H. lankadiva* in India and gives measurements and notes on its colour variation : this author suggests that in India the species is perhaps not subspecifically separable.

DISTRIBUTION : Ceylon ; Peninsular India.

Hipposideros lankadiva lankadiva Kelaart

Hipposideros lankadiva Kelaart, 1850b : 216, Kandy, Ceylon.

DISTRIBUTION : Ceylon.

Hipposideros lankadiva indus Andersen

Hipposideros indus Andersen, 1918 : 382. Gersoppa, Kanara, India.

Hipposideros lankadiva mixtus Andersen

Hipposideros indus mixtus Andersen, 1918 : 382. Kolar, eastern Mysore, India.

The available material of this and the other subspecies of *H. lankadiva* is very limited, but there seems little difference between *H. l. indus* and *H. l. mixtus* and they are likely to prove synonymous.

Hipposideros lankadiva unitus Andersen

Hipposideros indus unitus Andersen, 1918 : 382. Mundra, Saugor, Central Provinces, India, 1,600 feet.

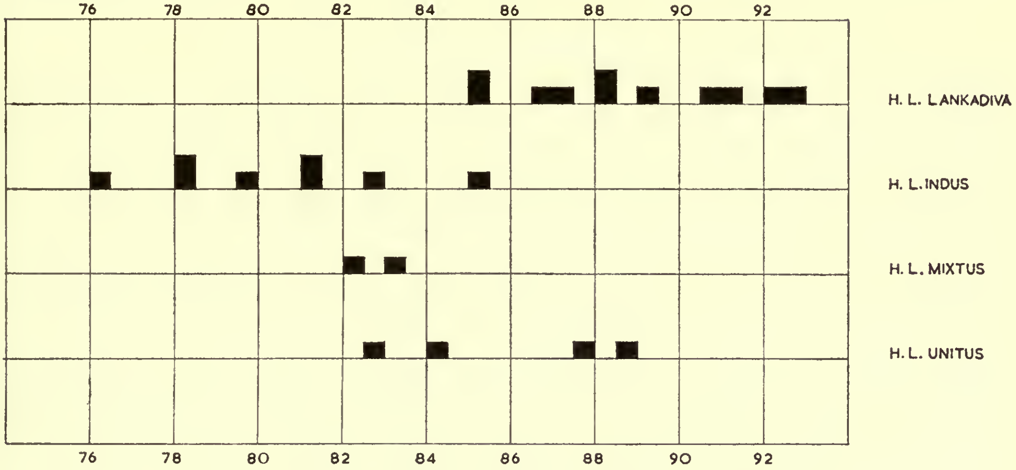


FIG. 35. Length of forearm in *Hipposideros lankadiva*

Hipposideros schistaceus Andersen

Hipposideros schistaceus Andersen, 1918 : 382. Vijayanagar, Bellary, India.

Andersen gave only a brief diagnosis of this species. Its ears and noseleaf are exactly as in *H. lankadiva* but its coloration is paler and less brown and the skull, although resembling that of *H. lankadiva* very closely, is smaller, less massive, lower and flatter : the cranial crests are less developed and the cochleae are comparatively wider, their width equal to their distance apart. The remaining features of the skull, and its dentition, exactly resemble *H. lankadiva*. *Hipposideros schistaceus* is evidently very closely related to *H. lankadiva*, differing from this species chiefly in its smaller, less massive skull and relatively larger bullae. The

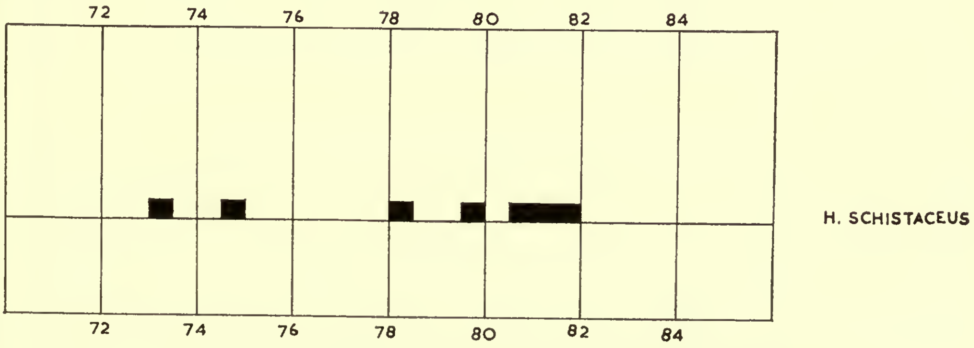


FIG. 36. Length of forearm in *Hipposideros schistaceus*

available material, both of *H. schistaceus* and of the smaller subspecies of *H. lankadiva*, is too limited to determine the extent of size variation in either *H. schistaceus* or *H. lankadiva*, and for the present their exact relationship must remain uncertain.

Hipposideros diadema

The ears are of moderate size, broad at the base and acutely pointed, with their posterior margins concave behind the tip. The noseleaf is well developed, with three or four lateral supplementary leaflets, the fourth small and sometimes rudimentary. The anterior leaf has no median emargination and the internarial septum is not inflated. The narial lappets are well developed and the nostrils are slightly pocketed. The intermediate part of the leaf is expanded with a prominent median ridge forming a median projection, flanked laterally by two much smaller projections. The posterior leaf is high, thick and fleshy, its upper edge semicircular, with a small median projection, and is supported by a median septum and two weak lateral septa. There is no frontal sac. The skull is large, its characters mainly those of the group. The cranial crests are moderately developed, the postorbital processes rounded and there is a shallow frontal depression. The rostral eminences are moderately inflated, the naso-frontal region from its dorsal aspect rounded and not pentagonal. The premaxillae make a wedge-shaped or slightly rounded junction with the maxillae and partially or wholly enclose the slightly elongate anterior palatal foramina. The palation is U-shaped or slightly V-shaped with the vomer projecting only very slightly beyond the posterior edge of the palate. The pterygoids and sphenoidal bridge are wide, almost completely concealing the elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are moderate, their width as great or nearly as great as their distance apart. The upper incisors are bilobed, the outer lobe usually a little larger than the inner lobe and are closely approximated with their tips convergent. The upper canines are not grooved anteriorly, and have no posterior cusps. The anterior upper premolar (pm^2) is small, partially or wholly extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is obsolescent or obsolete. The crown area of the outer lower incisors is considerably greater than that of the inner pair, while the anterior lower premolar (pm_2) is one half to two thirds the length and height of the second lower premolar (pm_4).

Hipposideros diadema has been divided into numerous subspecies over its extensive range, which includes almost the entire Indo-Australian region. As Tate (1941 : 373 et seq.) recognized, two broad groups of subspecies can be discerned among them. One group, composed of larger subspecies, is confined to the Asiatic mainland, Sumatra, Borneo, Java and their adjacent islands : the other, composed of smaller subspecies, is distributed from Celebes and the Philippine Islands eastwards to the Solomon Islands and northern Australia. There is some overlap between the two groups and larger subspecies are found in the Moluccas on the islands of Ceram and Batchian. Although in general the larger subspecies occur in the western parts of the range of *H. diadema* and the smaller towards the eastern limits of its distribution, there appears to be little evidence of a clinal pattern of size variation.

Distribution : Burma, Nicobar Islands and Philippine Islands east to the Solomon Islands and northern Australia.

Hipposideros diadema diadema (Geoffroy)

Rhinolophus diadema Geoffroy, 1813 : 263, pls. 5, 6. Timor Island.
Rhinolophus nobilis Horsfield, 1823 : No. 6, pl. Java.

Distribution : Timor Island ; Sumbawa Island ; Java.

Hipposideros diadema masoni (Dobson)

Phyllorhina masoni Dobson, 1872 : 338. Moulmein, Burma.
Hipposideros diadema vicarius Andersen, 1905 : 499. Sarawak.

According to Andersen (1905 : 500) *Phyllorhina masoni* Dobson is of uncertain application but later (1907 : 6) he recognized it as a subspecies of *H. diadema* and gave brief diagnostic characters to separate this from the nominate subspecies. There appear to be no grounds for the separation of specimens from the Asiatic mainland from those of Borneo and Sumatra when large series are examined. Osgood (1932 : 221) gives notes on specimens from Annam and Shamel (1942 : 322) compares specimens from Siam with those from Java.

Distribution : Burma ; Indochina : Annam (Osgood (1932 : 221)) ; Tonkin ; Siam (Shamel (1942 : 322)) ; Tenasserim ; Malay Peninsula ; Borneo ; Sumatra ; Nias Island (Miller (1942 : 117)).

Hipposideros diadema nicobarensis (Dobson)

Phyllorhina nicobarensis Dobson, 1871 : 262. Nicobar Islands, Bay of Bengal.

Hipposideros diadema enganus Andersen

Hipposideros diadema enganus Andersen, 1907 : 8. Engano Island.

Sody (1940 : 394) considers *H. d. enganus* to be a synonym of *H. d. masoni.*

Hipposideros diadema natunensis Chasen

Hipposideros diadema natunensis Chasen, 1940 : 43. Bunguran Island, North Natuna Islands.

Hipposideros diadema griseus (Meyen)

Rhinolophus griseus Meyen, 1833 : 608, pl. 46. San Matheo Cave, Montalban, near Manila, Luzon, Philippine Islands.
Hipposideros diadema anderseni Taylor, 1934 : 246. Novaliches, Rizal Province, Luzon.

Lawrence (1939 : 53) commented on the status of *H. d. anderseni.*

Distribution : Philippine Islands : Mindoro ; Cebu ; Mindanao ; Catanduanes ; Leyte ; Luzon ; Guimaras.

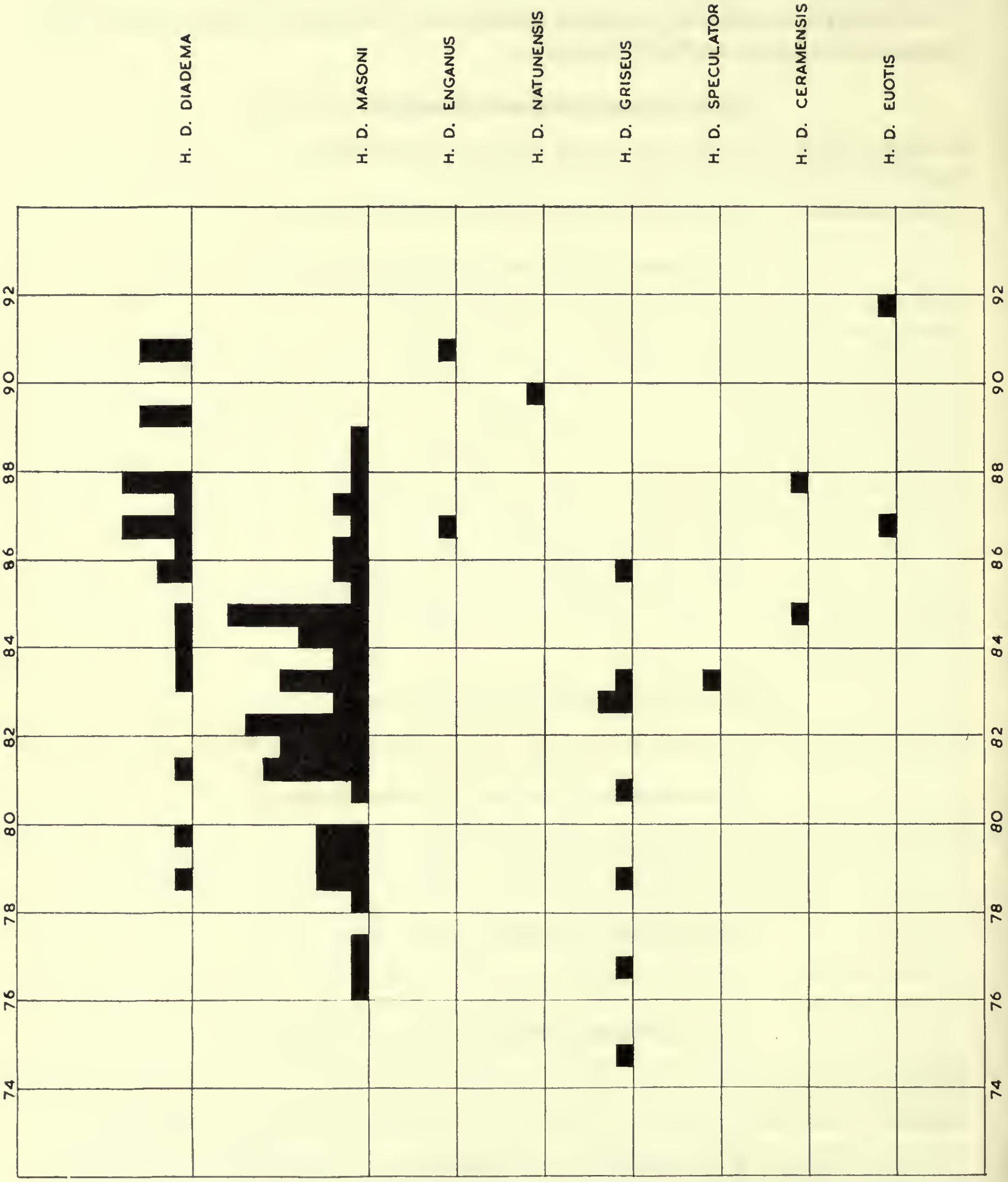


FIG. 37. Length of forearm in *Hipposideros diadema*

Hipposideros diadema speculator Andersen

Hipposideros diadema speculator Andersen, 1918 : 381. Kalao Island, Flores Sea, south of Celebes.

DISTRIBUTION : Celebes ; Kalao Island.

Hipposideros diadema ceramensis Laurie & Hill

Hipposideros diadema ceramensis Laurie & Hill, 1954 : 58. Teleoti Bay, south Ceram Island, Molucca Islands.

DISTRIBUTION : Molucca Islands : Ceram ; Buru.

Hipposideros diadema euotis Andersen

Hipposideros euotis Andersen, 1905 : 502. Batchian Island, Molucca Islands.

Hipposideros diadema pullatus Andersen

Hipposideros diadema pullatus Andersen, 1905 : 498. Haveri, Papua, 700 metres.

DISTRIBUTION : New Guinea.

Hipposideros diadema custos Andersen

Hipposideros diadema custos Andersen, 1918 : 381. Ara, Kei Island.

Hipposideros diadema mirandus Thomas

Hipposideros demissus mirandus Thomas, 1914 : 437. Manus Island, Admiralty Islands.

Hipposideros diadema trobrius Troughton

Hipposideros diadema trobrius Troughton, 1937 : 276. Kiriwina Island, Trobriand Islands.

Hipposideros diadema oceanitis Andersen

Hipposideros diadema oceanitis Andersen, 1905 : 497. Guadalcanar, Solomon Islands.

DISTRIBUTION : Solomon Islands : Guadalcanar ; Fauro ; Vella Lavella ; Ysabel ; Bougainville.

Hipposideros diadema demissus Andersen

Hipposideros demissus Andersen, 1909 : 268. Yanuta, San Christoval Island, east Solomon Islands.

Hipposideros diadema reginae Troughton

Hipposideros diadema reginae Troughton, 1937 : 275. Bloomfield River, Cooktown area, Queensland, Australia.

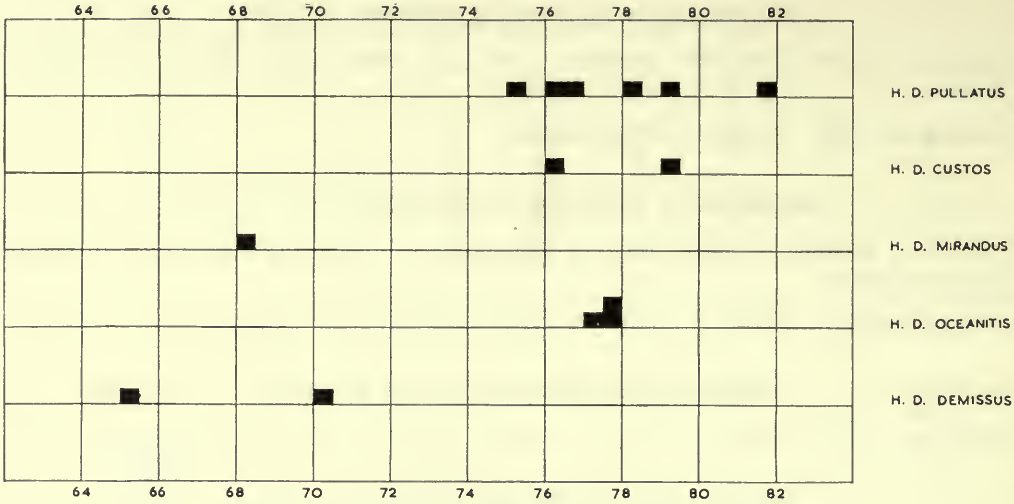


FIG. 38. Length of forearm in *Hipposideros diadema*

Hipposideros dinops

The ears are large, broad at the base and acutely pointed, their posterior margins concave just behind the tip. The noseleaf is large, with three lateral supplementary leaflets, the third small. The anterior leaf is broad and has no median emargination while the internarial septum is not inflated, the narial lappets are well developed and the nostrils slightly pocketed. The intermediate part of the leaf is expanded, with a prominent projecting median eminence, flanked laterally by much lesser swellings. The posterior leaf is thick and fleshy, its upper edge semicircular with a small, incipient median projection, and is supported by a median septum and two weak lateral septa. There is no frontal sac in the female type specimen. The skull is large, with well-developed lambdoid and sagittal crests. The postorbital processes are rounded and project very slightly, and there is a shallow frontal depression. The rostral eminences are moderately inflated and the rostrum is broadened, the naso-frontal region from its dorsal aspect very slightly less rounded and more angular than in *H. diadema*. The zygomata are moderate, with a prominent jugal process, and the anteorbital foramen is large, elongate and closed by a narrow bar. The premaxillae make a V-shaped contact with the maxillae and do not enclose or only just enclose the elongate anterior palatal foramina. The palation is U-shaped, the vomer projecting only very slightly beyond the posterior edge of the palate. The mesopterygoid fossa is wide and the pterygoids expanded, with the wide sphenoidal bridge almost completely concealing elongate lateral apertures. There is a shallow sphenoidal depression and the cochleae are a little wider than their distance apart. The mandible is massive, with a high coronoid process and with the massive angular process flexed slightly outwards. The upper incisors are strong and almost in contact, weakly bilobed, while the upper canines are massive and lack anterior or posterior cusps. The anterior upper premolar (pm^2) is small and extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact, while the posterior ridge of the third upper molar is almost obsolete. The crown area of the outer lower incisors is considerably greater than that of the inner pair and the anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4). *Hipposideros dinops* differs principally from *H. diadema* in its greater size, more greatly developed intermediate noseleaf, more angular naso-frontal region, more expanded zygomata and larger teeth. It is closely related to *H. diadema* and although evidently presenting some of the features of *H. diadema* in more exaggerated form, its angular, slightly pentagonal naso-frontal region, expanded zygomata and massive mandible are clearly correlations of the trend towards great size. In this respect, *H. dinops* links *H. diadema* to the giant species *H. inexpectatus* and displays to some extent the specializations of this species and of the more remotely related large African species *H. commersoni*.

DISTRIBUTION : Celebes ; Peleng Island ; Solomon Islands.

Hipposideros dinops dinops Andersen

Hipposideros dinops Andersen, 1905 : 502. Rubiana Island, Solomon Islands.

DISTRIBUTION : Solomon Islands : Rubiana ; Bougainville.

Hipposideros dinops pelingensis Shamel

Hipposideros pelingensis Shamel, 1940 : 353. Peleng Island, east of Celebes.

Hipposideros pelingensis Shamel is unrepresented in the collections of the British Museum (Natural History) but there seems very little doubt from its brief description that it is only subspecifically related to *H. dinops*. The tibia of *H. d. pelingensis* is shorter than that of *H. d. dinops* and Shamel says of the upper incisors that they " are small and bicusped, their inner cusps larger than the outer ones ". In the type specimen of *H. d. dinops* the outer lobes of the upper incisors are slightly larger than the inner lobes. Tate (1941 : 374) referred a series from south Celebes to *H. d. pelingensis* and noted that in size they were almost as large as *H. d. dinops* from Rubiana Island. Apparently with reference to this series, Tate stated that the premaxillae do not wholly enclose the anterior palatal foramina : in the type specimen of *H. d. dinops* these apertures are just enclosed by the anterior enclosing processes of the premaxillae.

DISTRIBUTION : Peleng Island ; Celebes (Tate (1941 : 374, 387, 391)).

Hipposideros inexpectatus Laurie & Hill

Hipposideros inexpectatus Laurie & Hill, 1954 : 60. Posso (=Poso), north Celebes.

A very large species, with ears similar to those of *H. diadema*, very large and broad at the base, acutely pointed and with their posterior margins concave just behind the tip. The noseleaf is very large and has four lateral supplementary leaflets : the third leaflet is reduced and the fourth minute. The anterior leaf is broad and has no median emargination. The internarial septum is not inflated and the narial lappets are well developed. The intermediate part of the leaf is greatly expanded with its central part much swollen and inflated but with only a very low, indefinite median ridge which does not extend to the upper margin of the intermediate part of the leaf : the swollen central part is flanked laterally by lesser eminences. The posterior leaf is thick and fleshy, its upper edge semicircular with a very small, incipient median projection and is supported by a narrow median septum and rather broader, less definite lateral septa. The skull is very large, with greatly developed lambdoid crests and an enormously developed, crescentic sagittal crest, merging into prominent supraorbital ridges. The postorbital processes project slightly and there is a shallow frontal depression. The rostral eminences are moderately inflated and the rostrum is broad, the naso-frontal region from its dorsal aspect slightly pentagonal, less rounded and more angular than in *H. diadema* or *H. dinops.* The zygomata are massive, greatly expanded and have a prominent jugal process, while the anteorbital foramen is very large and elongate, closed by a long, narrow bar. The premaxillae make a shallowly V-shaped junction with the maxillae and just enclose the slightly elongate anterior palatal foramina. The palation is U-shaped, the vomer projecting very slightly beyond the posterior edge of the palate, with wide mesopterygoid fossa, expanded pterygoids and large, wide sphenoidal bridge almost completely concealing elongate lateral apertures. There is a shallow sphenoidal depression and the width of the cochleae is a little greater than their distance apart. The mandible is massive, with a deep symphysis, high coronoid process and a thick, substantial angular process flexed strongly outwards. The upper incisors are large, their tips almost in contact and are weakly bilobed while the upper canines are massive and lack anterior or posterior cusps. The anterior upper premolar (pm^2) is small and extruded from the toothrow, the canine and the second upper premolar (pm^4) in contact. The posterior ridge of the third upper molar is obsolescent. The crown area of the outer lower incisors is considerably greater than that of the inner pair, and the anterior lower premolar (pm_2) is one half the length and height of the second lower premolar (pm_4).

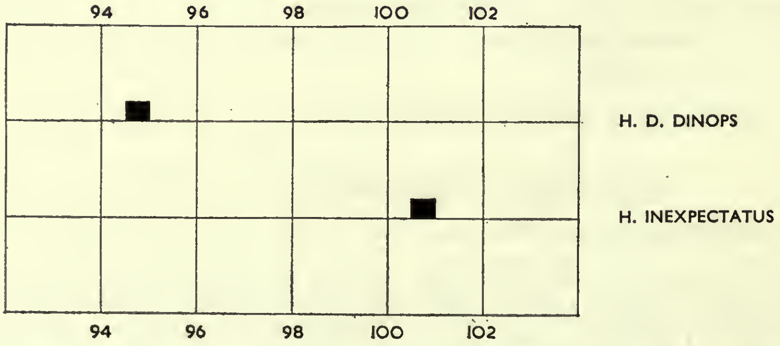


FIG. 39. Length of forearm in *Hipposideros dinops* and *H. inexpectatus*

Hipposideros inexpectatus is evidently closely related to *H. dinops*, but it differs from that species in its larger size, in its slightly less specialized intermediate noseleaf, which has no definite median ridge or projection as in *H. dinops* and in the greater development of those cranial specializations associated with great size. The skull of *H. inexpectatus* is larger than that of *H. dinops*, with more greatly developed cranial crests, a more angular, slightly pentagonal naso-frontal region and a much more massive mandible, and in these features approaches the large African species *H. commersoni*. Its broad ears, closely approximated upper incisors and the absence of a groove in the anterior faces of the upper canines ally it indubitably to *H. diadema* and *H. inexpectatus* is evidently an extreme of the trend towards great size of which *H. dinops* is a part.

Hipposideros commersoni

A very large species with the ears narrow at the base, triangular, rounded at the tips and with their posterior margins concave just behind the tip. The noseleaf is large and not greatly specialized, with three or four lateral supplementary leaflets, the fourth small, sometimes rudimentary and rarely but on occasion absent. The anterior leaf is broad and has no median emargination and the internarial septum is not inflated, while the narial lappets are well developed and the nostrils are slightly pocketed. The intermediate part of the leaf is expanded, with a low, indefinite median ridge or eminence and lacking lateral inflations. The posterior leaf is of moderate height, its upper edge flattened, without a median thickening or projection, and is supported by a median septum and two very weak lateral septa. A frontal sac is present in both sexes, its opening more or less longitudinal. The skull is large, with well-developed lambdoid crests and a greatly developed sagittal crest merging into sharply defined supraorbital ridges. The postorbital processes project slightly and the rostral eminences are moderately inflated. The rostrum is broad and the naso-frontal region from its dorsal aspect is distinctly pentagonal in outline. The zygomata are strong with a prominent jugal process, and the anteorbital foramen is large, elongate and closed by a narrow bar. The premaxillae make a V-shaped junction with the maxillae and wholly enclose the slightly elongate anterior palatal foramina. The palation is U-shaped, rather square, the vomer not projecting beyond the posterior edge of the palate. The mesopterygoid fossa is moderate and the pterygoids slightly constricted posteriorly, while the sphenoidal bridge is moderate, not excessively constricted, partially concealing elongate lateral apertures. There is a well-developed sphenoidal depression and the width of the cochleae is a little greater than their distance apart. The mandible is massive, with a deep symphysis, high coronoid process and a substantial angular process, flexed strongly outwards. The upper incisors are very weakly bilobed and set widely apart, at the outer margins of the premaxillae, while the upper canines have their anterior faces shallowly grooved and have low posterior cusps. The anterior upper premolar is very small, extruded from the toothrow, with the canine and the second upper premolar (pm^4) in contact or nearly so. The posterior ridge of the third upper molar is obsolete or almost obsolete. The crown area of the outer lower incisors is a little greater than that of the inner pair, while the anterior lower premolar (pm_2) is one half or less the length and height of the second lower premolar (pm_4).

Hipposideros commersoni stands rather sharply apart from the Asiatic species of the group by virtue of its narrower ears, pentagonal naso-frontal region, widely separated upper incisors and grooved upper canines, which possess low posterior cusps. Although in some respects *H. commersoni* is approached by the large Australasian species *H. dinops* and *H. inexpectatus*, these are basically species of the *diadema* type which appear to have developed specializations similar to those of *H. commersoni* as correlations of their large size, and *H. commersoni* must be regarded as a species of rather remote origin in the *diadema* group.

DISTRIBUTION : Madagascar ; eastern Africa south to Nyasaland and Northern Rhodesia ; Southwest Africa and Angola north to Gambia ; Congo.

Hipposideros commersoni commersoni (Geoffroy)

Rhinolophus commersoni Geoffroy, 1813 : 263, pl. 5. Fort Dauphin, Madagascar.

DISTRIBUTION : Madagascar.

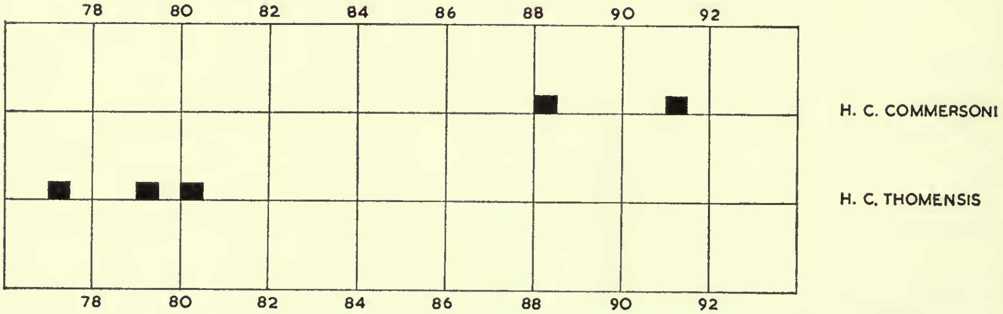


FIG. 40. Length of forearm in *Hipposideros commersoni*

Hipposideros commersoni marungensis (Noack)

Phyllorhina commersoni var. *marungensis* Noack, 1887 : 272, pl. 10, figs. 31–33. Qua-Mpala, Marungu, western Tanganyika.
Hipposideros commersoni mostellum Thomas, 1904a : 385. Tana River, Kenya.

DISTRIBUTION : Kenya ; Tanganyika ; Zanzibar ; Nyasaland ; Northern Rhodesia ; Southwest Africa.

Hipposideros commersoni gigas (Wagner)

Rhinolophus gigas Wagner, 1845 : 148. Benguela, Angola.
Phyllorrhina vittata Peters, 1852 : 32, pl. 6, figs. 1–3, pl. 13, figs. 7–13. Ibo Island, Cap Delgado group, 12° 20′ S. (in part, male co-type only : lectotype selected by Andersen (1906a : 45)).
(?) *Hipposideros gigas gambiensis* Andersen, 1906a : 42. Gambia.
Hipposideros gigas viegasi Monard, 1939 : 70. Madina Boé, Portuguese Guinea.

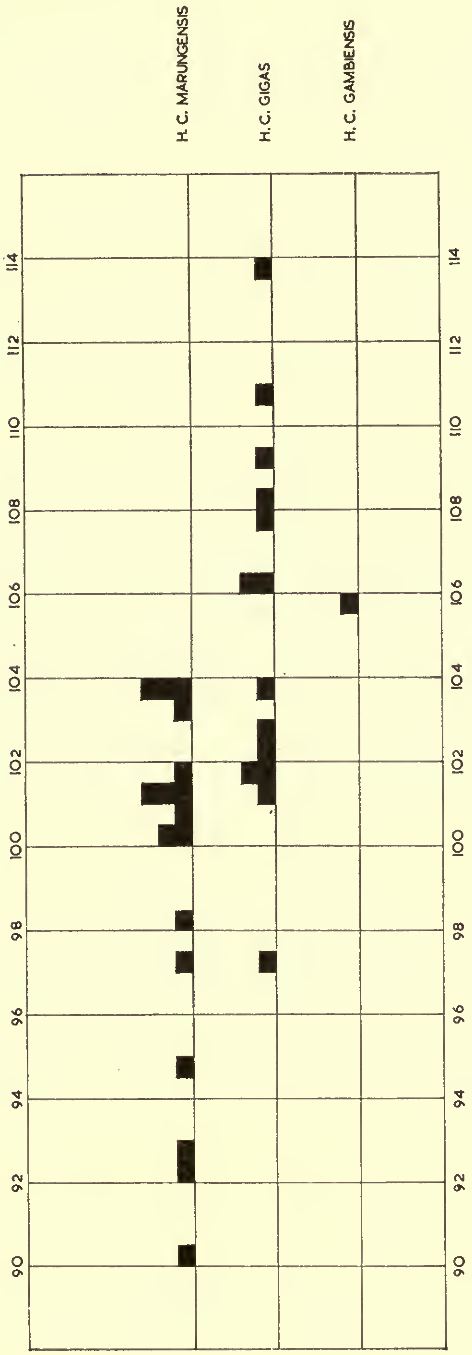


FIG. 41. Length of forearm in *Hipposideros commersoni*

Hipposideros gigas gambiensis was separated from *H. c. gigas* by Andersen on the grounds of slightly wider noseleaves. It seems unlikely to be a valid subspecies.

Distribution : Angola ; Congo (part) ; Tanganyika (part) ; Cameroons ; Nigeria ; Ghana ; Guinea ; Portuguese Guinea ; Gambia.

Hipposideros commersoni thomensis (Bocage)

Phyllorhina commersoni var. *thomensis* Bocage, 1891 : 88 and 1905 : 67. San Thomé Island.

Hipposideros commersoni niangarae J. A. Allen

Hipposideros gigas niangarae J. A. Allen, 1917 : 438, pl. 51, fig. 1. Niangara, Uele district, Congo.

SUMMARY

The genus *Hipposideros* presents a wide range of morphological variation, and the characters of its numerous species rarely combine to indicate clearly defined natural groups or evolutionary trends. This revision, based chiefly on the features of the ears, noseleaf and skull, discusses the morphological criteria within the genus and its supraspecific groupings, recognizing seven species groups containing a total of forty-three species. These groups and their included species are described in some detail, with keys, and their probable relationships have been defined and discussed. These studies have suggested a less diffuse classification of *Hipposideros* than those proposed by earlier revisers, and indicate that despite the wide morphological dissimilarity of many of its species, the genus includes but three major evolutionary trends.

ACKNOWLEDGEMENTS

My thanks are due to Mr. H. M. van Deusen, Curator of the Archbold Collections of the American Museum of Natural History, who arranged the loan of specimens ; to Dr. G. B. Corbet, for his valuable suggestions on the presentation of data ; to Mr. R. W. Hayman, whose knowledge of Africa and of African bats has been readily available and to Miss Annette Bown, who prepared the illustrations and diagrams used in this paper.

TABLE 2—Summary of cranial measurements of *Hipposideros*

	Number of specimens	Condylocanine length	Number of specimens	Rostral width	Number of specimens	Interorbital width	Number of specimens	Zygomatic width	Number of specimens	Mastoid width	Number of specimens	Length of maxillary toothrow (c-m^3)
H. megalotis . . .	4	11·6–12·9 (12·3)	4	3·2–3·7 (3·4)	4	2·0–2·2 (2·1)	1	6·9	3	6·9–7·5 (7·1)	4	4·2–4·8 (4·5)
H. bicolor pomona . .	1	14·6	1	4·4	1	2·7	1	8·4	1	9·1	1	5·7
H. bicolor gentilis . .	25	14·5–15·9 (15·2)	34	4·1–4·7 (4·5)	30	2·4–2·9 (2·7)	24	8·3–9·0 (8·7)	26	8·7–9·3 (9·0)	34	5·8–6·2 (5·9)
H. bicolor sinensis . .	2	15·5–15·6	7	4·4–4·6 (4·5)	4	2·5–2·7 (2·5)	2	8·6–8·7	2	9·1–9·4	7	5·9–6·2 (6·0)
H. bicolor atrox . . .	7	15·4–15·9 (15·6)	10	4·4–4·6 (4·5)	9	2·3–2·8 (2·5)	8	8·6–9·4 (9·2)	7	8·9–9·1 (9·0)	11	6·2–6·5 (6·3)
H. bicolor major . .	1	16·1	1	4·7	1	3·0	1	9·5	1	9·3	1	6·5
H. ater ater . . .	18	13·2–13·9 (13·6)	26	3·7–4·3 (4·0)	26	2·1–2·5 (2·3)	21	7·9–8·3 (8·0)	21	8·1–8·5 (8·2)	26	5·1–5·5 (5·3)
H. ater nicobarulae . .	3	14·2–15·0 (14·6)	3	4·3–4·4 (4·4)	3	2·4–2·7 (2·5)	2	8·4–8·6	2	8·6–8·8	3	5·7–5·9 (5·8)
H. ater saevus . . .	16	13·5–14·7 (14·1)	18	3·9–4·5 (4·1)	18	2·2–2·7 (2·5)	17	7·5–8·4 (8·0)	16	8·2–8·5 (8·3)	18	5·1–5·7 (5·5)
H. ater antricola . . .	2	13·7–14·7	2	4·1–4·2	2	2·3	1	8·3	2	8·2–8·4	2	5·3–5·8
H. ater aruensis . .	1	13·7	3	3·9–4·1 (4·0)	2	2·4–2·6	1	8·2	1	8·4	2	5·2–5·4
H. ater gilberti . . .	2	13·5–13·9	2	4·0	2	2·0–2·2	2	7·9–8·2	2	8·2–8·4	2	5·3–5·4
H. fulvus fulvus . .	9	15·5–16·0 (15·8)	10	4·3–4·7 (4·5)	9	2·3–2·8 (2·6)	8	9·0–9·6 (9·3)	9	8·8–9·3 (9·1)	10	6·2–6·7 (6·4)
H. fulvus pallidus . .	17	15·0–16·4 (15·5)	21	4·2–4·6 (4·4)	21	2·2–2·7 (2·4)	21	8·6–9·6 (9·1)	18	8·6–9·1 (8·9)	21	6·0–6·8 (6·3)
H. cineraceus cineraceus .	20	12·7–13·7 (13·2)	24	3·5–4·1 (3·8)	24	2·1–2·8 (2·5)	20	7·0–7·6 (7·3)	21	7·6–8·1 (7·8)	24	4·8–5·2 (5·0)

TABLE 2—Summary of cranial measurements of *Hipposideros* (*Continued*)

	Number of specimens	Condylocanine length	Number of specimens	Rostral width	Number of specimens	Interorbital width	Number of specimens	Zygomatic width	Number of specimens	Mastoid width	Number of specimens	Length of maxillary toothrow (c-m³)
H. cineraceus micropus	1	12·6	1	3·5	1	2·5		—	1	8·0	1	4·9
H. nequam		—	1	5·2		—		—		—	1	6·3
H. calcaratus	5	19·0–19·5 (19·2)	8	5·1–5·2 (5·2)	8	3·4–3·8 (3·6)	8	10·7–11·6 (11·3)	7	9·7–10·5 (10·1)	8	7·9–8·4 (8·2)
H. cupidus	1	16·7	2	4·4–5·0	2	3·2–3·9	2	9·6–10·4	2	9·5–10·0	2	7·2–7·3
H. ridleyi	1	17·1	1	5·9	1	3·0	1	9·4	1	10·6	1	6·6
H. jonesi	2	16·0–16·7	2	4·8–5·0	2	2·8–3·0	2	8·3–8·5	2	10·0–10·1	2	5·9–6·2
H. dyacorum	1	14·1	3	4·3–4·5 (4·4)	2	2·5–2·6	2	9·2–9·5	1	8·7	3	5·4–5·6 (5·5)
H. sabanus	1	12·9	2	3·5–3·6	2	2·2–2·3	1	8·8	1	8·1	2	5·1
H. obscurus		—	1	4·9	1	2·5	1	9·4	1	9·2	1	6·6
H. pygmaeus		—	1	4·1		—		—		—	1	5·0
H. galeritus galeritus	2	15·7–15·8	5	4·5–5·2 (4·9)	4	2·7–2·9 (2·8)	2	9·7–10·1	3	9·0–9·2 (9·1)	5	6·3–6·6 (6·5)
H. galeritus brachyotus	7	14·1–15·5 (14·7)	8	4·6–5·1 (4·8)	8	2·5–2·8 (2·7)	9	8·4–9·2 (8·8)	8	8·5–9·2 (8·8)	10	5·4–5·9 (5·7)
H. galeritus schneideri	2	15·2–15·5	2	4·9–5·4	2	2·6–3·2	2	9·8–10·4	2	9·0–9·1	2	6·2–6·4
H. galeritus labuanensis	19	15·0–16·0 (15·6)	28	4·8–5·3 (5·1)	25	2·5–2·9 (2·7)	20	9·1–10·4 (9·9)	19	8·7–9·6 (9·3)	27	6·2–6·8 (6·5)
H. galeritus cervinus	37	13·8–14·9 (14·3)	45	4·1–5·0 (4·4)	43	2·2–2·8 (2·4)	38	8·6–9·7 (9·2)	39	8·2–8·8 (8·6)	44	5·4–6·3 (5·9)
H. breviceps	2	14·4	2	5·1–5·2	2	3·0	2	9·3–9·7	2	8·8	2	5·6–5·8
H. curtus	1	14·7	2	4·7–4·8	2	2·7–2·8	1	8·9	1	9·4	2	5·3–5·5
H. fuliginosus	2	20·3–20·5	3	5·9–6·4 (6·1)	3	3·3–3·7 (3·5)	2	12·0–12·9	2	11·5	3	8·0–8·6 (8·3)

H. caffer caffer	73	14·0–15·2 (14·6)	92	4·1–4·7 (4·4)	86	2·3–3·2 (2·7)	76	8·6–9·5 (9·0)	83	8·8–9·5 (9·2)	87	5·4–6·2 (5·7)
H. caffer tephrus	8	14·1–14·5 (14·4)	8	4·1–4·3 (4·2)	7	2·6–2·8 (2·6)	7	8·5–8·9 (8·7)	8	8·7–9·1 (9·0)	8	5·5–5·8 (5·6)
H. caffer ruber	41	15·2–17·2 (15·9)	44	4·2–5·1 (4·5)	41	2·8–3·3 (3·0)	36	9·2–10·7 (9·9)	42	8·9–10·4 (9·8)	44	6·2–6·9 (6·4)
H. caffer angolensis	19	15·0–15·9 (15·5)	22	4·4–4·8 (4·6)	20	2·4–2·9 (2·7)	17	9·0–10·0 (9·3)	19	9·0–9·7 (9·4)	22	5·8–6·4 (6·2)
H. caffer guineensis	39	15·3–16·9 (15·8)	48	4·3–5·0 (4·8)	46	2·6–3·3 (3·0)	43	9·2–10·7 (10·2)	49	9·1–10·3 (9·8)	49	6·1–7·0 (6·7)
H. beatus	3	13·9–14·4 (14·0)	4	4·2–4·6 (4·4)	4	2·5–3·0 (2·8)	3	9·2–9·5 (9·4)	3	8·6–9·0 (8·8)	4	5·6–5·9 (5·7)
H. coxi	1	16·9	1	5·9	1	3·3	1	9·3	1	10·2	1	6·4
H. papua	1	16·7	1	5·8	1	3·0	1	11·0	1	9·4	1	7·5
H. cyclops	26	23·0–26·2 (24·5)	27	7·9–8·8 (8·2)	27	2·7–3·6 (3·2)	25	14·3–16·1 (15·2)	27	11·3–12·6 (12·0)	27	9·7–10·8 (10·2)
H. camerunensis	2	25·9–27·1	2	9·6–9·7	2	3·4–3·7	2	16·3–16·4	2	12·9–13·2	2	9·8–11·1
H. muscinus	1	16·3	1	5·8	1	2·5	1	10·7	1	8·9	1	7·1
H. wollastoni	1	15·1	1	5·7	1	2·2	1	9·3	1	8·0	1	6·4
H. semoni	5	16·3–17·3 (16·8)	7	5·6–6·3 (6·0)	8	1·8–2·4 (2·0)	7	10·4–11·1 (10·8)	4	8·4–9·2 (8·7)	9	6·5–7·3 (6·9)
H. stenotis		—	1	5·1	1	2·1		—	1	7·8	1	5·6
H. pratti	2	27·7–27·9	2	10·5	2	4·5	2	16·9–17·5	2	15·3–15·5	2	11·9–12·0
H. lylei	15	24·9–25·9 (25·3)	15	9·3–10·0 (9·7)	15	3·9–4·8 (4·3)	12	14·5–16·0 (15·3)	14	13·0–14·2 (13·8)	15	10·5–11·3 (10·8)
H. armiger armiger	45	26·4–29·8 (28·0)	63	8·8–10·4 (9·6)	52	3·3–4·7 (4·1)	49	16·1–19·3 (17·6)	49	14·0–16·1 (14·9)	64	11·1–12·8 (12·1)
H. turpis turpis	3	23·0–23·1 (23·0)	8	7·4–7·8 (7·6)	8	3·3–3·6 (3·4)	3	14·1–14·5 (14·3)	3	12·9–13·1 (13·0)	8	9·7–10·2 (10·0)
H. turpis pendleburyi	1	23·6	1	7·9	1	3·8	1	15·0	1	13·1	1	10·1
H. abae	8	19·8–20·8 (20·4)	9	5·7–5·9 (5·8)	9	2·9–3·8 (3·4)	7	13·2–14·5 (13·7)	9	11·4–12·6 (11·9)	9	8·7–9·0 (8·9)
H. larvatus larvatus	17	18·5–19·8 (19·3)	21	5·9–6·4 (6·2)	19	2·9–3·2 (3·1)	18	11·7–12·8 (12·2)	18	10·5–10·9 (10·8)	21	8·1–8·7 (8·5)
H. larvatus neglectus	3	20·0–20·6 (20·2)	3	6·5–6·7 (6·7)	3	3·2–3·5 (3·4)	3	12·8–13·8 (13·2)	3	10·8–11·7 (11·3)	3	8·6–9·1 (8·8)
H. larvatus grandis	29	19·1–21·5 (20·4)	31	6·4–7·3 (6·9)	30	3·0–3·7 (3·3)	28	12·1–13·7 (13·1)	29	10·8–11·8 (11·3)	31	8·3–9·5 (8·9)

TABLE 2—Summary of cranial measurements of *Hipposideros* (*Continued*)

	Number of specimens	Condylocanine length	Number of specimens	Rostral width	Number of specimens	Interorbital width	Number of specimens	Zygomatic width	Number of specimens	Mastoid width	Number of specimens	Length of maxillary toothrow (c-m³)
H. larvatus leptophyllus	8	20·9–21·4 (21·1)	8	7·4–7·7 (7·6)	8	2·8–3·3 (3·1)	8	13·4–14·0 (13·6)	8	11·6–12·2 (11·9)	8	8·9–9·4 (9·1)
H. speoris speoris	28	16·1–17·5 (16·8)	41	5·0–5·5 (5·2)	38	2·7–3·2 (2·9)	29	10·5–11·7 (11·0)	29	9·5–10·3 (9·9)	42	6·8–7·5 (7·1)
H. speoris pulchellus	18	15·8–17·3 (16·4)	17	5·0–5·4 (5·2)	18	2·6–3·2 (2·8)	18	10·1–11·1 (10·6)	18	9·3–10·4 (9·7)	18	6·7–7·2 (6·9)
H. lankadiva lankadiva	3	30·3–30·8 (30·6)	8	8·8–9·3 (9·1)	8	3·5–3·8 (3·7)	5	19·2–20·6 (19·8)	3	15·0–15·9 (15·5)	7	13·7–14·4 (14·0)
H. lankadiva indus	6	26·7–27·5 (27·2)	8	7·9–8·4 (8·1)	8	3·2–3·6 (3·4)	6	16·9–19·9 (17·8)	7	13·6–14·4 (14·2)	8	12·1–13·1 (12·6)
H. lankadiva mixtus	2	27·2–27·7	2	7·8–8·0	2	3·3–3·7	2	17·5–18·0	2	14·4	2	12·2–12·3
H. lankadiva unitus	3	27·6–28·0 (27·9)	3	8·4–8·5 (8·5)	4	3·3–3·7 (3·5)	3	17·9–18·3 (18·1)	3	14·3–14·4 (14·4)	4	12·6–13·1 (12·9)
H. schistaceus	3	25·0–25·2 (25·1)	4	7·1–7·7 (7·4)	4	3·3–3·5 (3·5)	2	15·8–16·0	4	12·9–13·2 (13·1)	4	11·0–11·6 (11·3)
H. diadema diadema	12	27·1–30·0 (28·5)	16	8·8–9·7 (9·1)	15	3·3–4·1 (3·7)	11	17·0–19·6 (19·0)	12	14·0–15·5 (14·9)	16	11·8–13·5 (12·7)
H. diadema masoni	8	27·7–29·4 (28·4)	16	8·6–9·6 (9·1)	15	3·0–3·9 (3·6)	11	17·2–19·5 (18·4)	8	14·0–15·3 (14·7)	16	12·0–13·6 (12·6)
H. diadema enganus	1	29·2	1	9·9	1	3·6		—		—	2	13·1–13·8
H. diadema natunensis	1	28·6	1	9·8	1	3·9	1	18·6	1	14·6	1	13·3
H. diadema griseus	3	26·0–27·9 (26·8)	5	8·0–8·5 (8·3)	5	2·9–3·6 (3·4)	5	15·9–17·1 (16·5)	5	13·7–14·7 (14·3)	5	11·2–12·6 (11·8)
H. diadema speculator	2	27·2–27·6	2	9·1	2	3·8–4·0	2	16·8–17·6	2	14·3	2	11·9–12·2
H. diadema ceramensis	1	29·3	1	9·1	2	4·0–4·3	2	18·2–19·1	2	15·6–16·1	2	12·5–13·4

H. diadema euotis . .		—	3	10·2–10·6 (10·4)	2	3·8–4·0	1	19·3		—	3	13·0–13·5 (13·3)
H. diadema pullatus . .	6	26·0–27·5 (26·5)	8	8·7–9·1 (8·9)	8	3·1–3·7 (3·5)	6	16·9–17·8 (17·3)	7	14·0–14·7 (14·4)	8	11·3–12·1 (11·8)
H. diadema custos . .	1	28·2	1	9·0	1	3·3	1	18·0	1	14·5	1	12·6
H. diadema mirandus . .	1	24·8	2	8·0	2	3·2–3·3	2	15·1–15·4	2	13·3	2	10·7
H. diadema oceanitis . .	2	26·6–27·1	3	8·1–8·4 (8·2)	3	3·5–3·6 (3·6)	3	16·9–17·7 (17·1)	3	14·0–14·1 (14·0)	3	11·0–11·7 (11·4)
H. diadema demissus . .		—	2	7·5–7·9	2	3·2–3·4	2	14·7–15·2		—	2	10·2–10·9
H. dinops dinops . .	1	32·5	1	10·4	1	3·6	1	20·7	1	16·5	1	14·2
H. inexpectatus . . .	1	34·7	1	11·7	1	3·7	1	22·4	1	18·4	1	15·2
H. commersoni commersoni .	2	27·1–27·6	4	7·9–8·9 (8·5)	4	2·8–3·4 (3·1)	3	15·2–16·8 (16·1)	3	13·8–14·0 (13·9)	4	10·1–11·0 (10·7)
H. commersoni marungensis .	14	28·5–31·8 (30·2)	16	9·0–10·4 (9·6)	15	3·1–4·0 (3·6)	15	17·4–19·9 (18·6)	15	14·5–18·0 (15·6)	15	11·5–12·6 (12·0)
H. commersoni gigas . .	5	30·9–33·7 (32·2)	10	9·5–11·4 (10·5)	7	3·5–4·7 (3·8)	5	17·2–20·7 (19·5)	5	14·4–17·8 (16·3)	10	13·0–14·0 (13·5)
H. commersoni thomensis .		—	3	8·7–8·8 (8·7)	3	3·0–3·2 (3·1)	3	16·5–16·6 (16·5)	3	12·8–14·0 (13·4)	3	10·9–11·3 (11·0)

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S. K. BHATTACHARYYA

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A REVISION OF THE BRITISH MITES OF THE GENUS *PERGAMASUS* BERLESE S.LAT. (ACARI: MESOSTIGMATA)

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BY

S. K. BHATTACHARYYA

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A REVISION OF THE BRITISH MITES OF THE GENUS *PERGAMASUS* BERLESE S.LAT. (ACARI: MESOSTIGMATA)

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INTRODUCTION

Mites of the family Parasitidae, in its present concept, were included in the genus *Gamasus* Latr. until Berlese (1892) subdivided the genus into three subgenera, *Gamasus* s. str., *Eugamasus* Berl. and *Hologamasus* Berl. This division was based primarily on the form of the sclerotization of the idiosoma in the adult female and the nature of the gnathosomal corniculi in the male. In 1904, Berlese proposed three other subgenera, namely, *Trachygamasus* (type *Gamasus pusillus* Berl.), *Pergamasus* (type *Acarus crassipes* Linn.) and *Amblygamasus* (type *Gamasus tiberinus* Can.) although these were not defined until Berlese (1906) published his " Monografia del Genere *Gamasus* ". The genus *Trachygamasus* was characterized by the absence of metasternal shields in the female (actually the metasternals are completely fused with each other and the sternal shields) while the two other subgenera were essentially based on the armature of the second pair of legs in the male.

Berlese's concepts of the classification of the '*Gamasus*'-complex have been subject to little revision subsequently although each of his subgenera has, at one time or another, been given generic rank. Hull (1918) for example, recognized Berlese's groupings but gave generic rank to *Ologamasus*, *Pergamasus* and *Gamasus*, whilst he considered *Amblygamasus* to be a subgenus of *Pergamasus*, and *Eugamasus* a subgenus of *Gamasus*. This author also proposed a further division of *Pergamasus* and erected the subgenera *Paragamasus* and *Plesiogamasus*. Since Berlese's monograph four genera have also been added to the family, namely, *Oocarpais* Berlese, 1916, *Parasitellus* Willmann, 1939, *Gamasodes* Oudemans, 1939 and *Pergamasellus* Evans, 1957. Certain nomenclature changes have also been necessary, such as *Parasitus* Latr. having priority over *Gamasus* Latr. and *Holoparasitus* Oudemans 1936 being proposed as a new name for *Ologamasus* Berlese, 1892 *non* Berlese, 1888.

The contributions to the knowledge of the Parasitidae within the past forty years have largely been in the form of descriptions of new species with little or no attempt at critical revisions at generic level. European workers have been particularly prominent in the field, new species having been described, amongst others, by Oudemans (1902, 1904, 1912, and 1926), Voigts and Oudemans (1904), Bonnet (1911), Hull (1916 and 1918), Halbert (1915), Trägårdh (1910 and 1936), Vitzthum (1926), Willmann (1932, 1938, 1939, 1940, 1949, 1951, 1953, 1954 and 1956), Sellnick (1929, 1940), Pax & Willmann (1937), Leitner (1946 & 1946a), Cooreman (1943, 1951), Schmolzer (1953), Halaskova (1959) and Schweizer (1961). Schweizer's key to the Parasitidae of Switzerland, published posthumously in 1961, has been the only attempt at a complete regional revision of the family since Hull (1918).

This work presents a revision of the British mites of the genus *Pergamasus* Berl. s. lat. Members of this genus are amongst the most important acarine predators in Palaearctic soils although they appear to be replaced by the Rhodacaridae in tropical soils (Evans, *in litt.*). The confusion concerning the identity of the species of this relatively large genus limits the scope of ecological work on the rôle played by these mites in the arthropod community of the soil. Although Turk (1953) lists twenty-four species and varieties of *Pergamasus* (including *Amblygamasus*, *Paragamasus* and *Plesiogamasus*) for the British Isles only a small percentage of these can be identified with certainty. It is intended that this work will remedy, in part, this confusing situation and also, by the detailed study of the external morphology of the species, provide new criteria for their classification.

The type material is deposited in the Collections of the British Museum (Natural History).

METHODS

This revision is largely based on identified and unidentified specimens of *Pergamasus* in the Collections of the British Museum (Natural History). This material was supplemented by Berlese-Tullgren extractions of litter and other organic debris made by the author.

The specimens were prepared for microscopical study by clearing them in 60% lactic acid. All the figures have been made from temporary preparations in lactic acid. Structures requiring detailed study, for example leg II of the male, chelicerae, pedipalps and the genital shield of the female, were dissected and prepared separately. Specimens were orientated in cavity slides for studying structures situated laterally, for example the peritreme and peritrematal shield.

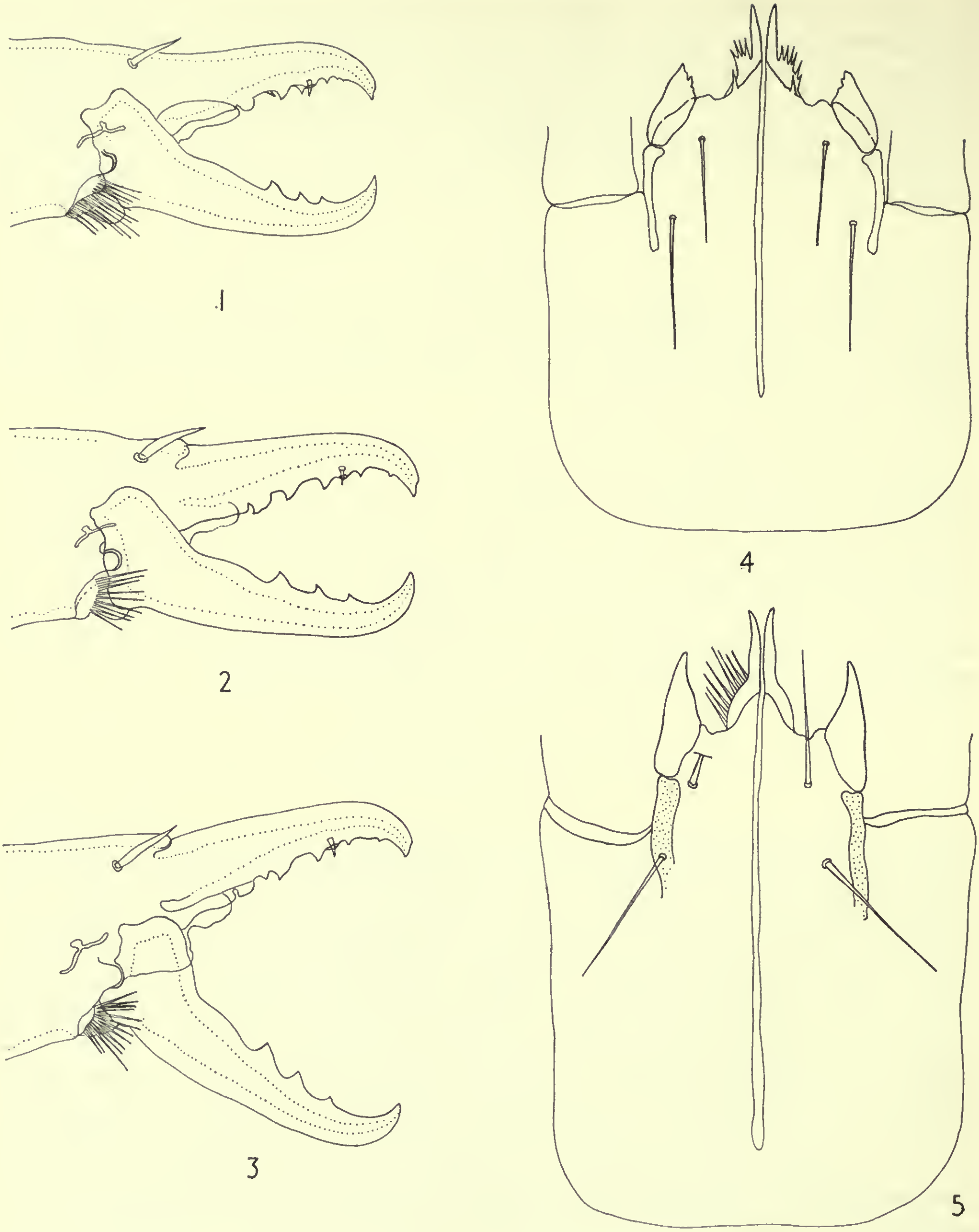
The three species cultured under laboratory conditions were confined in small petri dishes containing a charcoal and Plaster of Paris base of the type used by Bhattacharyya (1962). They fed on various species of Collembola.

EXTERNAL MORPHOLOGY

Chelicerae

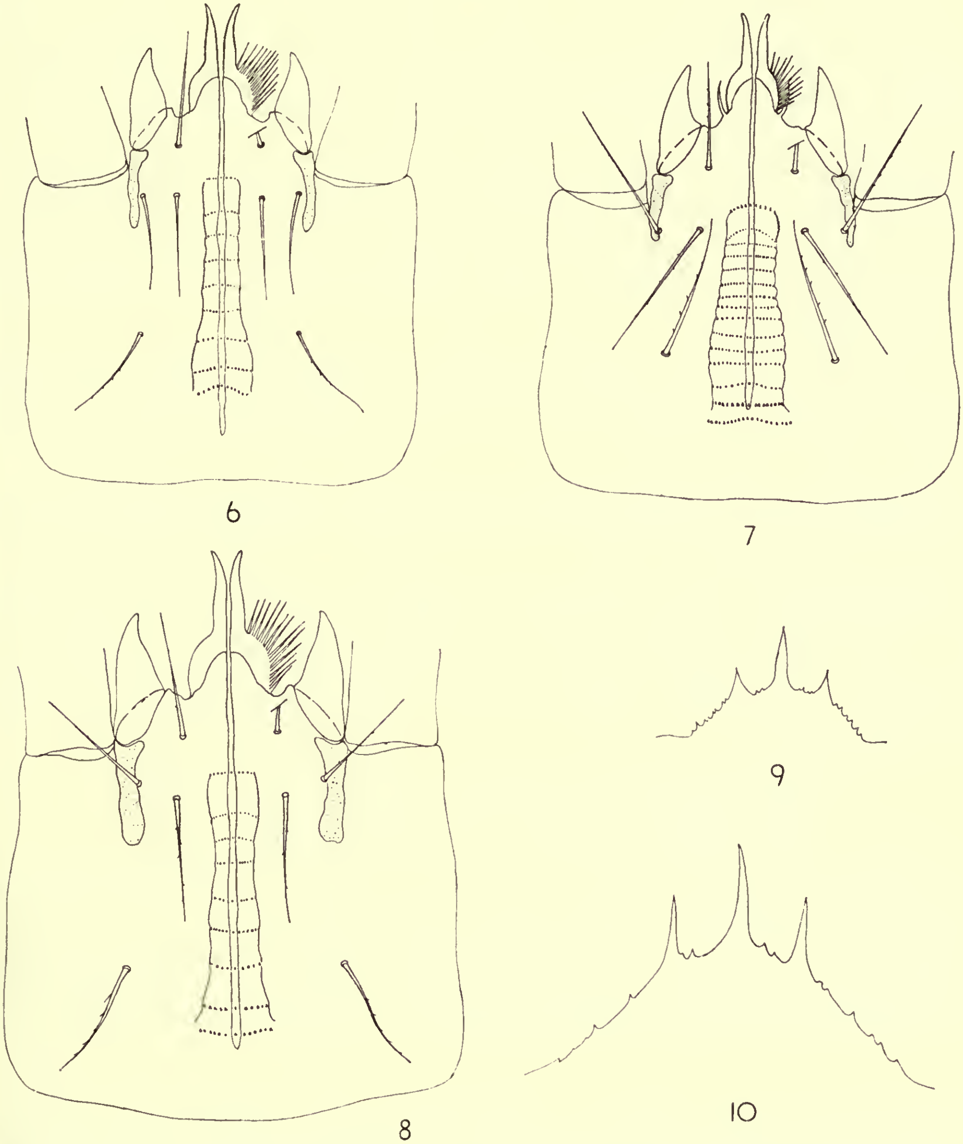
The chelicerae are three-segmented with the basal segment short, the second segment long and terminating in the fixed digit, and the third segment represented by the movable digit. Both digits are invariably dentate. The movable digit in the male and females of the *Paragamasus*-group of species bears one, two or three well-defined teeth (Text-figs. 185, 228) whilst in the *Pergamasus*-group the dentition is more variable. The pilus dentilis is simple in all species examined. The shape and number of teeth on the fixed digit of both groups shows considerable interspecific variation; the number of teeth ranging from one to several. A simple (Text-fig. 256), comb-like or spatulate (Text-fig. 106) dorsal seta is present as well as two lyriform fissures. The fixed digit in certain males is truncated distally, for example in *Pergamasus runciger* Berlese (Text-fig. 262) and *P. diversus* Halbert (Text-fig. 166). The spermadactyl is simple and fused with the movable digit distally (Text-fig. 206). The processes of the arthrodial membrane at the base of the movable digit may be simple or branched (Text-figs. 247 & 185) ; branched processes being rare in the females.

The ontogenetic development of the dentition of the digits of the chelicerae in *Pergamasus robustus* (Oudems.) is shown in Text-figures 1, 2 and 3. It will be noted that in *P. robustus* the dentition of the movable digit is constant throughout the



Figs. 1–5. Figs. 1–3, Chelicerae of the larva (fig. 1), protonymph (fig. 2), and deutonymph (fig. 3) of *Pergamasus* (*Paragamasus*) *robustus* (Oudemans). Figs. 4 and 5. Gnathosoma of the larva (fig. 4) in *Pergamasus* (*Pergamasus*) *septentrionalis* (Oudemans) and (fig. 5) in *Pergamasus* (*Paragamasus*) *robustus* (Oudemans).

post-embryonic developmental stages. In *P. septentrionalis* (Oudems.), on the other hand, there is a progressive addition of teeth to the digit up to the deutonymph. The dorsal seta is constant in form throughout ontogeny.



Figs. 6–10. Figs. 6–8 : Gnathosoma of the protonymph (fig. 6) of *Pergamasus* (*Paragamasus*) *robustus* (Oudemans), protonymph (fig. 7) of *Pergamasus* (*Pergamasus*) *septentrionalis* (Oudemans) and deutonymph (fig. 8) of *Pergamasus* (*Paragamasus*) *robustus*. Figs. 9–10 : Tectum of the protonymph (fig. 9) and deutonymph (fig. 10) of *P.* (*P.*) *robustus*.

Gnathosomal base, hypostome, tectum and pedipalps

The gnathosomal base and hypostome are well developed. The chaetotaxy of the venter of the hypostome comprises three setae in the larva, one of which has hypertrophied to form horn-like corniculi. The other two setae (gs.1 and gs.2) are simple or slightly pilose (Text-figs. 4 & 5). In the protonymph two pairs of setae are added, namely gs.3 on the venter of the hypostome and gs.4 on the gnathosomal base (Text-figs. 6 & 7). This chaetotaxy is retained in the deutonymph (Text-fig. 8) and adult (Evans, 1957). Setae gs.2 and gs.3 normally form a more or less transverse row between gs.1 and gs.4 ; the exception occurs in some males, where gs.3 lies anterior to gs.2. The corniculi in females and immature stages are sessile but in males they are borne on stalk-like projections of the hypostome which bear the hypostomal setae (Text-fig. 102). The hypostomal processes are strongly developed and show interspecific differences. Their external margins are invariably fringed with setae-like processes.

The deutosternum in the adults bears eight to fifteen transverse rows of denticles. There are no deutosternal denticles in the larva. With few exceptions the number of rows of denticles is constant in the protonymph, deutonymph and adult of a given species.

The tectum in the adults is usually produced into three distinct prongs although this number may be increased to five or more in the neotrichous species. The form of the tectum is often markedly dissimilar in different post-embryonic stages of a species (Text-figs. 9 & 10).

The pedipalp has five free segments excluding the apotele which is represented by a three-tined seta-like structure on the inner basal angle of the tarsus. The chaetotaxy of the palp is an important taxonomic criterion both as regards the number of setae and their form. The palpal chaetotactic formulae are as follows (Text-figs. 11–13) :—

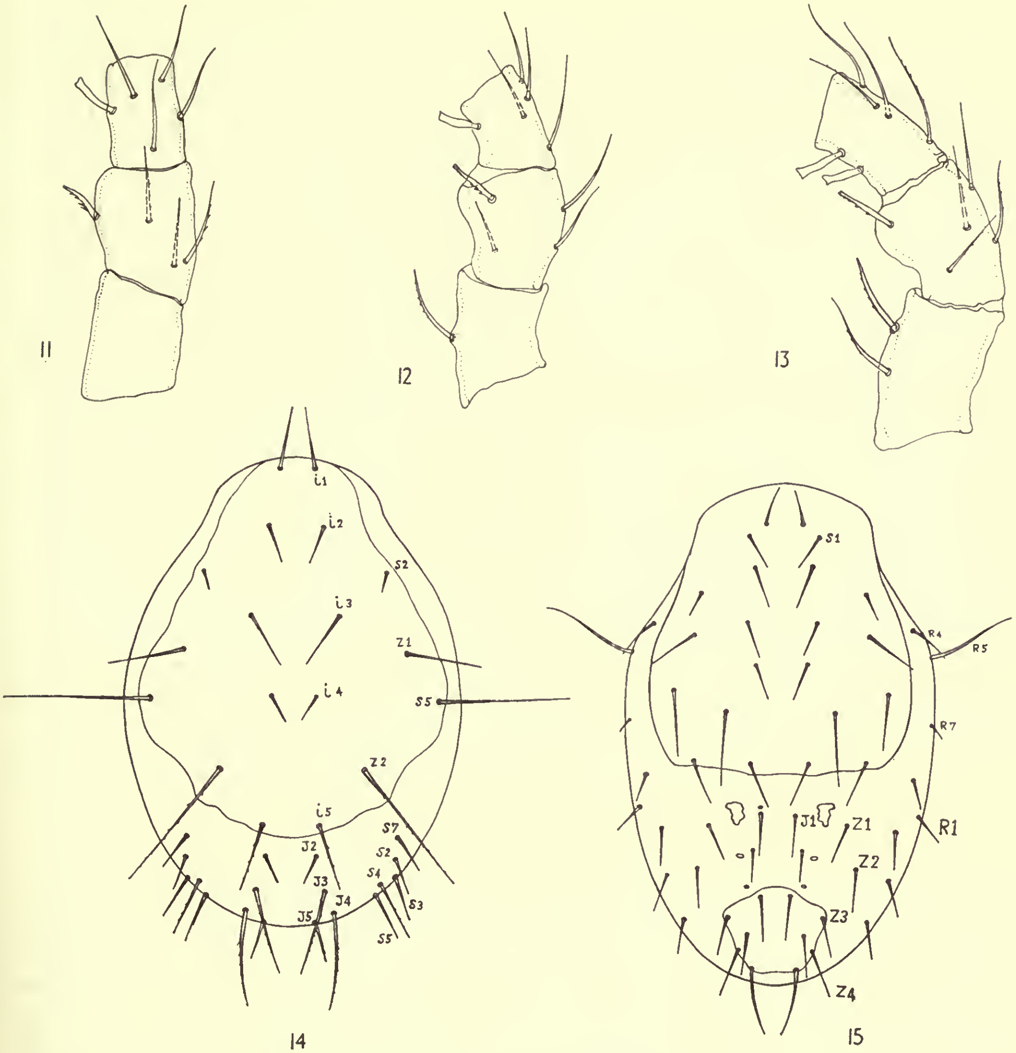
Larva (0–4–5–12–11–apotele).
Protonymph (1–4–5–12–15–apotele).
Deutonymph and adult (2–5–6–14–15–apotele).

In certain males the palp trochanter has one or two ventral protuberances ; the larger protuberance always bears a seta. Forms with two protuberances have the proximal one considerably smaller than the distal (Text-fig. 195). The seta on the internal (anterior) face of the femur is always comb-like whereas the two setae on the internal face of the genu may be spatulate or comb-like (Text-figs. 227 & 64). The other setae of these two segments may be simple or pilose.

Idiosoma

DORSUM

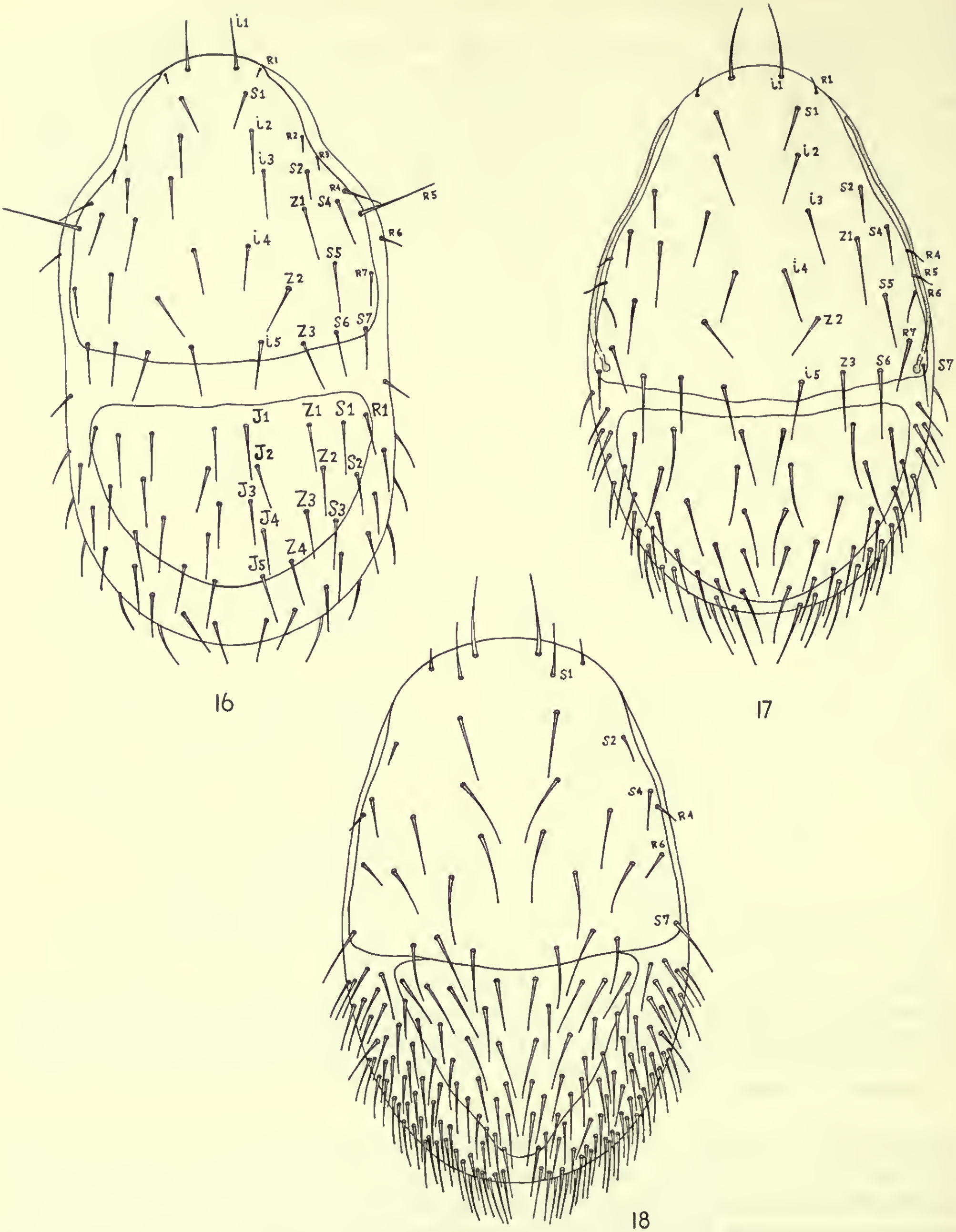
The dorsum of the larva has a well-defined podonotal shield bearing the normal nine pairs of setae (i1, i2, i3, i4, i5, z1, z2, s1 and s5). The unsclerotized cuticle posterior to the podonotal shield also carries nine setae comprising J2–J5, s7, S2–S5 (Text-fig. 14). In the protonymph, there are fifteen setae (including s7) in the podonotal region of which eleven setae are situated on the podonotal shield. The



FIGS. 11–15. Figs. 11–13 : Pedipalp of the larva (fig. 11), protonymph (fig. 12), and deutonymph (fig. 13) of *Pergamasus* (*Paragamasus*) *robustus* (Oudemans). Figs. 14 and 15 : Dorsum of the larva (fig. 14) and protonymph (fig. 15) of *Pergamasus* (*Paragamasus*) *robustus*.

setae added to this region of the dorsum in the protonymph are : s1, s6, r4, r5 and r7 (Text-fig. 15). Fourteen pairs of setae occur on the opisthonotal region of which four or five pairs may be situated on a small, weakly sclerotized opisthonotal shield (Text-fig. 15). Setae J1, Z1–Z4 and R1 are added at this stage. Mesonotal scutellae may be present or absent.

I have observed three types of chaetotaxy of the podonotal region in deutonymphs depending on the number of setae in the r series. In *P. robustus* twenty-one setae


i1
R1
S1
i2
R2
R3
i3
S2
R4
R5
Z1
S4
i4
R6
S5
Z2
R7
S6
S7
i5
Z3
J1
Z1
S1
R1
J2
Z2
S2
J3
Z3
S3
J4
Z4
J5
i1
R1
S1
i2
S2
i3
Z1
S4
R4
i4
R5
S5
R6
Z2
R7
i5
Z3
S6
S7
S1
S2
S4
R4
R6
S7

16

17

18

FIGS. 16–18. Dorsum of the deutonymph of *Pergamasus* (*Paragamasus*) *robustus* (Oudemans) (fig. 16), *Pergamasus* (*Pergamasus*) *crassipes* (L.) Berlese (fig. 17) and *Pergamasus* (*Pergamasus*) *septentrionalis* (Oudemans) (fig. 18).

are present in this region with the r series (r1–r7) complete (Text-fig. 16). *P. crassipes*, on the other hand, has nineteen setae, r2 and r3 being absent (Text-fig. 17) and *P. septentrionalis* only seventeen setae, r2, r3, r5 and r7 being absent (Text-fig. 18). There are probably more than these three types I have observed, particularly amongst the species showing neotrichy of the podonotal region in the adult, for example *Pergamasus mirabilis* Willmann and *Pergamasus hamatus* (Koch), but I have not seen deutonymphs of these species. The deutonymphal opisthonotal shield is invariably well-defined and in the *Paragamasus*-group bears twelve or thirteen pairs of setae. The thirteen setae present on the opisthonotal shield of *P. robustus*, for example, are J1–J5, Z1–Z4, S1–S3 and R1 (Text-fig. 16). Neotrichy affects the unsclerotized cuticle of the opisthonotal region and the opisthonotal shield of members of the *Pergamasus*-group (Text-figs. 17 & 18) to such an extent that it is not possible to distinguish the primary setae.

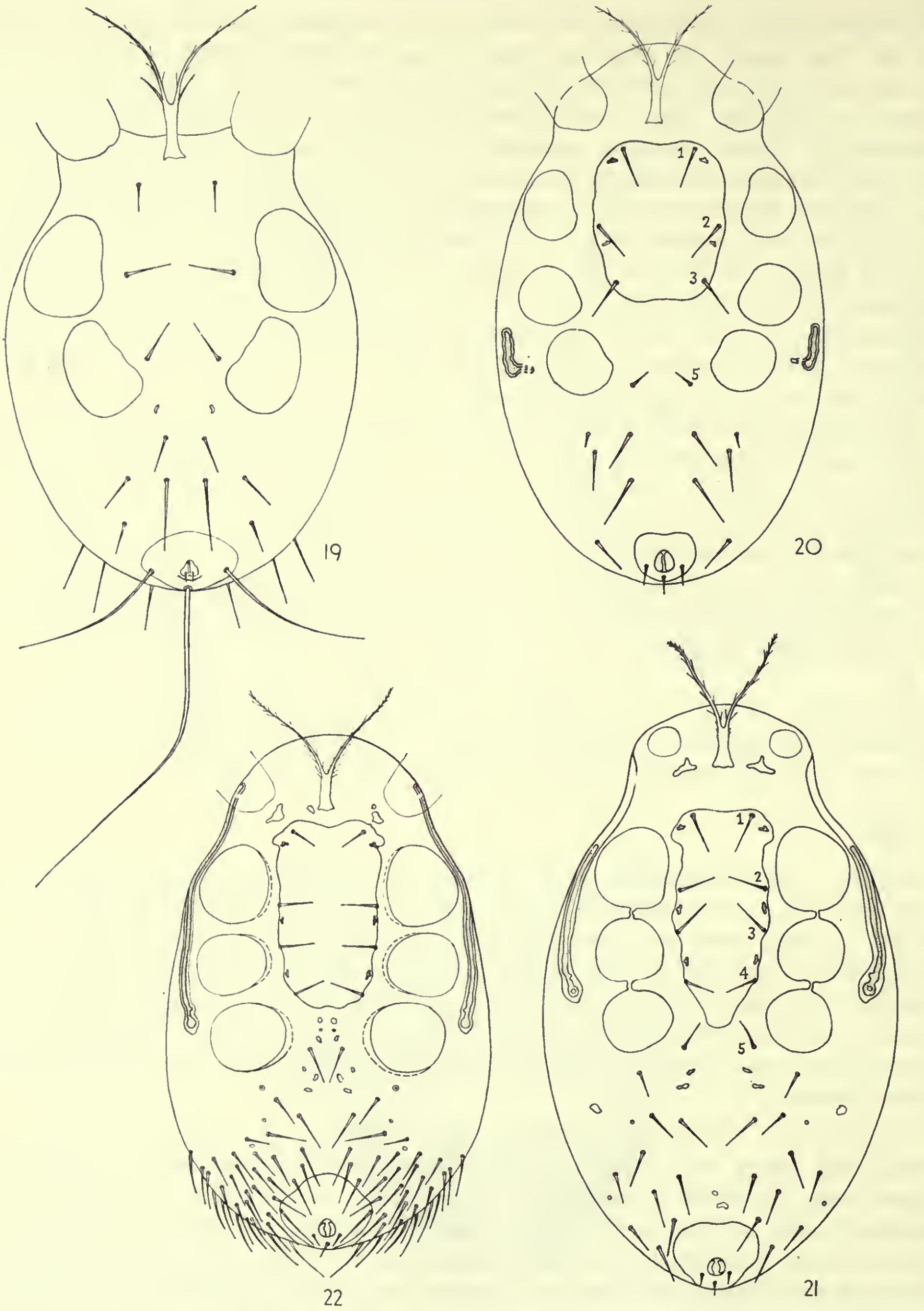
The dorsal chaetotaxy of the deutonymph of the *Paragamasus* group is retained by the adult and there is a fusion of the podonotal and opisthonotal elements to form an entire dorsal shield (Text-fig. 103). In the males of some species the line of fusion of these two sclerites is discernible (Text-fig. 96). The fusion of the deutonymphal podonotal and opisthonotal shield also occurs in the neotrichous *Pergamasus*-group and setae appear to be added to the dorsum at the deutonymphal ecdysis. The neotrichy is usually restricted to the opisthonotal region although in *P. hamatus* and *P. mirabilis* the podonotal region is also involved (Text-figs. 88 & 76).

The surface of the dorsal shield or shields is usually regionally reticulated and provided with numerous pore-like structures. The dorsal setae are usually simple although some pilose setae occur in immature and adult stages.

Venter

Larva : The tritosternum in the larva has a rectangular base, longer than wide and a pair of pilose laciniae (Text-fig. 19). The sternal region bears three pairs of simple or pilose setae but there is no definite indication of a sternal shield. All the species have a well-defined anal shield with the normal complement of setae, namely, a pair of paranals and a post-anal seta. These setae are invariably long. Each anal valve is provided with an euanal seta. The remainder of the opisthogastric region carries four pairs of setae distributed as in the Text-figure 19. There are no stigmata or peritremes.

Protonymph : The tritosternum is essentially the same as in the larva. The inter-coxal region bears four pairs of setae of which the anterior three pairs, homologous with the three sternal setae in the larva, are situated on a sternal shield provided with two pairs of lyriform fissures (Text-fig. 20). The remaining pair of setae situated between coxae IV is homologous with the genital setae of the adult. The anal shield bears the three setae present in the larva but these are considerably shorter in length. There are no euanal setae. The chaetotaxy of the remainder of the opisthogastric region shows an increase of one pair of setae which is located lateral to the anal shield. A pair of stigmata and short peritremes are present.



Figs. 19–22. Venter of the larva (fig. 19) of *Pergamasus* (*Paragamasus*) *robustus* (Oudemans), protonymph (fig. 20) of *Pergamasus* (*Pergamasus*) *crassipes* (L.) Berlese, deutonymph (fig. 21) of *P.* (*P.*) *robustus* and deutonymph (fig. 22) of *P.* (*P.*) *crassipes*.

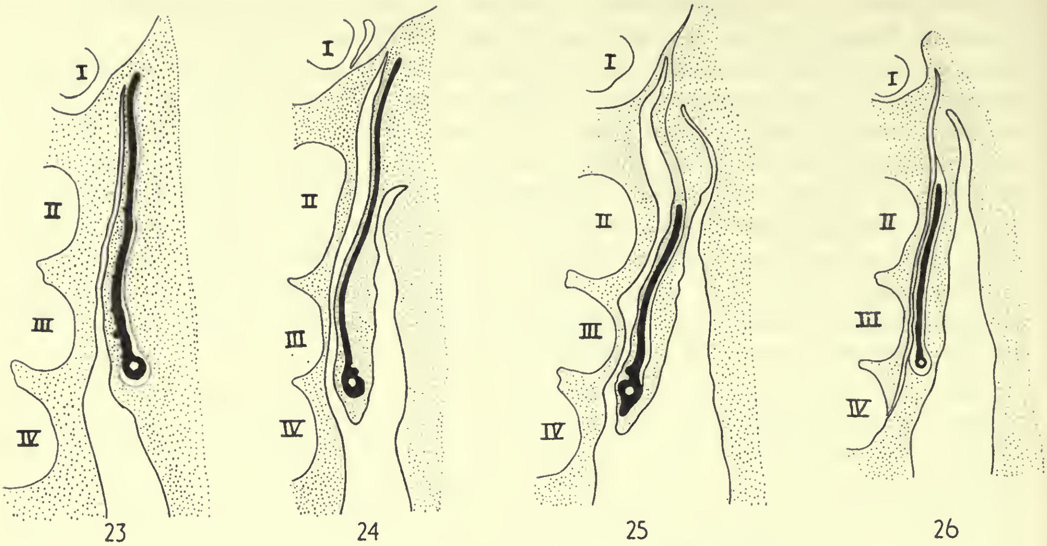
Deutonymph : The tritosternum is similar to that of the protonymph but is invariably flanked by one or more pairs of prae-endopodal shields. The inter-coxal region carries five pairs of setae ; those additional to the protonymphal complement being setae IV (the metasternals). Sternal setae I–IV are situated on a well-sclerotized sternal shield (Text-fig. 21). The anal shield is essentially the same as in the protonymph although in the *Pergamasus*-group some of the opisthogastric setae may be located on the shield. In the *Paragamasus*-group, unsclerotized cuticle of the opisthogastric region bears eight, nine or ten pairs of setae (Text-fig. 21), but in the *Pergamasus*-group neotrichy occurs particularly in the posterior region of the opisthogaster (Text-fig. 22). Both groups have well developed stigmata, peritremes and peritrematal shields. The length of the peritreme varies interspecifically. Small sclerites are often present on the opisthogaster.

Female : The tritosternum resembles that of the immature stages although the pilosity of the laciniae may be indistinct in some species. The prae-endopodal shields are well-defined in all the species examined but there is considerable inter-specific variation in their shape, size and number. All species have a sternal shield bearing three pairs of setae and two pairs of lyriform fissures. The sternal shield is fused with the exopodal shields between coxae I and II and with the endopodal shields in the region of coxae II and III. Its posterior margin is often deeply incised medially and its surface may be variously ornamentated with a network of lines or punctures. The metasternal setae are situated on large discrete metasternal shields which are fused with the endopodal elements in the region of coxae IV and flank the triangular genital shield. Rarely, the metasternal shields are weakly fused along the median line. They bear a pair of lyriform fissures.

The genital shield is large and with the exception of *Paragamasus suecicus* (Trägårdh) (Plate 7l) is broadly triangular in outline. It bears a pair of genital setae. The anterior portion of the shield is strengthened by more heavily sclerotized areas whose outlines are of taxonomic importance (Plate 7b and Plate 8d). The genital shield overlies the genital orifice and a pair of sclerites (paragynials) referred to as " nymphae " by Berlese (1906). The wall of the vagina is variously sclerotized, the sclerotization being in the form of endogynial processes (Text-fig. 70, 118). Some species also have a pair of horn-like structures extending beneath the meta-sternal shields.

The opisthogastric shield is large and is fused with the podal elements in the region of coxae IV. The anus is subterminal and paired paranal and the post-anal setae are always present. In the *Paragamasus*-group (Text-figs. 264, 217) the opisthogastric shield bears eight, nine or ten (Text-figs. 213, 123, 117) pairs of setae excluding those associated with the anus, whereas the number is markedly increased in the neotrichous species of the *Pergamasus*-group (Text-figs. 36 & 57).

The stigmata and peritremes are conspicuous ; the length of the peritreme shows interspecific variation. The peritrematal shield shows varying degrees of fusion with the dorsal shield and the opisthogastric shield. In *Pergamasus crassipes* (Linn.), *P. longicornis* (Berl.), *P. septentrionalis* (Oudems.) and *P. quisquiliarum* (Can.), the shield is completely fused with the dorsal shield (Text-fig. 23). In

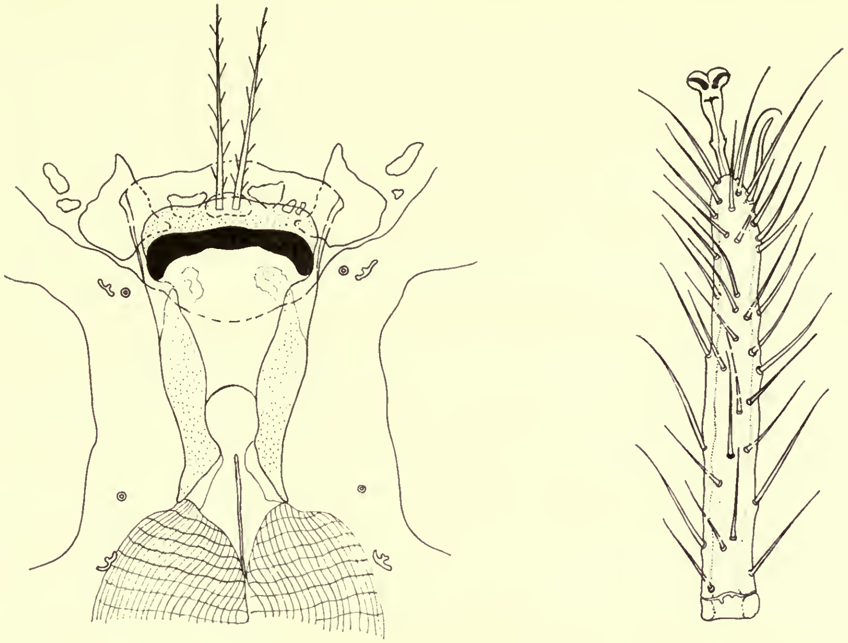


FIGS. 23–26. Peritrematal shields of females.
Fig. 23 *Pergamasus* (*Pergamasus*) *longicornis* Berlese, fig. 24 *Pergamasus* (*Pergamasus*) *hamatus* (Koch), fig. 25 *Pergamasus* (*Paragamasus*) *diversus* Halbert and fig. 26 *Pergamasus* (*Paragamasus*) *alstoni* sp. nov.

P. hamatus (Koch) and *P. hortensis* sp. nov. the extent of fusion with the dorsal shield is less ; the shield being free in its posterior half (Text-fig. 24). In the *Paragamasus*-group the shield is free (Text-fig. 25) or fused with the opisthogastric shield posteriorly (Text-fig. 26).

The unsclerotized cuticle of the opisthogastric region is provided with a variable number of setae.

Male : The dorsal, lateral and ventral surfaces of the idiosoma in the male are completely sclerotized except at the junction of the exo- and endopodal shields, between coxae II and III, and III and IV. The genital orifice is situated immediately anterior to the sternal shield and its ventral wall is strongly sclerotized (Text-fig. 27). The orifice is protected by a genital lamina whose anterior margin may be produced into one or two processes. The lamina is connected by a pair of elongate apodemes to strong retractor muscles and it is assumed that the lamina is capable of being withdrawn into the orifice. The base of the tritosternum, covered by the lamina, is strongly reduced but the pilose laciniae resemble those of the female. Praeendopodal shields are invariably present. The chaetotaxy of the venter of the male resembles that of the females of the same species. Sternal seta 5 (the genital) may be situated near (*P. diversus*, *P. alpestris*) or on (*P. lapponicus*, *P. teutonicus*) scalelike tubercles (Text-figs. 163, 193). The peritrematal shields (including the stigmata and peritremes) are entirely fused with the dorsal shield and the exopodals. A poststigmatic seta may or may not be present.



27 28

FIGS. 27–28. *Pergamasus* (*Paragamasus*) *lapponicus* Trägårdh, male.
Fig. 27 internal view of the sterniti-genital region. Fig. 28 tarsus and prae-tarsus of leg I.

Legs

The legs are six segmented (excluding the ambulacrum) in all post-embryonic developmental stages. Lyriform fissures occur in the basal half of the femora and tarsi, and result in false divisions of these segments. All the segments of the legs have a well-defined chaetotaxy which has been studied in detail by Evans (1963) whose terminology I have adopted. The chaetotaxy of each instar shows little or no intra or interspecific variation in setal complement although the relative lengths and form of the setae may vary. Leg II in the male is specialised for grasping the female during mating which, as in the majority of the Mesostigmata, is an indirect method involving a spermatophore. Leg II is often enlarged (crassate) and two setae (v_2 and v_3) on the femur and one on the genu (av_1) and the tibia (av_1) hypertrophy and form spur-like structures. The form of the spurs on these segments is of taxonomic importance. A dorsal seta on the basal half of tarsus IV is invariably long and erect. The ambulacrum comprises a lobed pulvillus and two claws (Text-fig. 28).

CLASSIFICATION

The *Paragamasus*-group is at present, divided into four subgenera. According to Hull (1918) these subgenera may be characterized as follows:—

1 'Body of both sexes piriform, rostrum very prominent, cuticle polished and smooth, Femur II of male crassate but spurless. Colour ruddy brown' . . . . *Amblygamasus* Berlese.

2 ' Body of both sexes piriform, cuticle conspicuously reticulate and rather rough. Femur II crassate with a strong falcate spur ; patella with a prominent apical spur or branch projecting inwards and forwards. Colour ruddy brown, rather dull ' . . . . . *Pergamasus* s. str.

3 ' Body oblong, more or less parallel sided in both sexes. Ped II as in (2) but without the patellar spur. Colour pale yellowish brown ' *Paragamasus* Hull.

4 ' Body of male narrow, oblong, of female rather piriform. Ped II of the male only slightly crassate all spurs more or less cylindrical. Colour very pale ' *Plesiogamasus* Hull.

The validity of Hull's subdivision of the genus must be assessed on the basis of the characters associated with leg II of the male since those based on the shape of the idiosoma and its colour are less reliable ; being subjected to considerable intraspecific variation. His reference to the armature of the patella is confusing. Assuming that his " patella " refers to the genual segment, then the prominent apical spur on leg II of *P. crassipes* (the type of the subgenus *Pergamasus*) is not located on that segment but on the tibia whereas in *P. alpestris*, which Hull includes in *Pergamasus* s. str., the characteristic L-shaped process is present on the genu. Thus, Hull's use of the armature of the patella in separating *Pergamasus* and *Paragamasus* has no foundation. Further, the statements that members of *Paragamasus* have no patellar spur is also inaccurate, the only British species of the genus without a spur on genu II are *P. quisquiliarum* and *P. diversus* and Hull considered that the latter should probably be placed in *Pergamasus* s. str.

The type species of *Paragamasus* Hull (type *Pergamasus robustus* (Oudemans)) and *Plesiogamasus* Hull (type *Pergamasus hamatus* (Koch) sensu Berlese, 1905) were designated by Turk & Turk (1952).

Within the limited number of species (thirty-two) I have examined the groupings formed on the basis of various combinations of external morphological characters indicate an intrageneric rather than an intergeneric relationship between the groups. The emphasis laid on the characters associated with leg II in the male in the classification at subgeneric level appears to be unwarranted. The nature of the armature of leg II does not appear to be correlated with any other distinctive morphological character and the degree of development of spurs (hypertrophied setae) and sclerotized protuberances show every gradation in form, from the weakly developed nodular spurs of *P. nathistmus* sp. nov. to the massive spurs and protuberances of *P. robustus* and *P. crassipes*.

The only character I have found which will give a reliable practical division of the genus is the chaetotaxy of the dorsum and the opisthogastric region of the idiosoma. Two groups are readily definable ; one in which the chaetotaxy displays neotrichy and the other in which neotrichy is not apparent. This character has the advantage over characters restricted to the male or female in being determined at the deutonymphal stage and of applying to both sexes. I have, provisionally, included the neotrichous species in the subgenus *Pergamasus* Berl. s. str. and the non-neotrichous species in *Paragamasus* Hull. These subgenera have the following characteristics :—

Family Parasitidae Oudemans

Genus **PERGAMASUS** Berlese, 1904 s. lat.

Type : ***Pergamasus crassipes*** (Linn.) Berlese, 1906.

Subgenus ***Pergamasus*** s. str.
(including *Amblygamasus* Berl. and *Plesiogamasus* Hull).

The chaetotaxy of the dorsum and of the opisthogastric region of the idiosoma displays neotrichy in all the members of this subgenus. With the exception of *P.* (*P.*) *hamatus*, neotrichy of the dorsal chaetotaxy is restricted to the opisthosomal region. Two distinct groups of species may be recognized on the basis of female characteristics, namely : the *crassipes*-group (*P.* (*P.*) *crassipes* and *P.* (*P.*) *longicornis ; P.* (*P.*) *septentrionalis* and *P.* (*P.*) *quisquiliarum*) in which the peritrematal shield is entirely fused with the dorsal shield in the region of coxae II–IV and the tectum is essentially five-pronged ; and the *hamatus*-group (*P.* (*P.*) *hamatus* and *P.* (*P.*) *hortensis*) in which the peritrematal shield is free posteriorly and the tectum is essentially three-pronged. The female of *P.* (*P.*) *mirabilis* is not known.

Members of the *crassipes*-group are large (up to 1,383μ), strongly sclerotized species ; the males of which may be readily distinguished by the armature of leg II and the form of the internal setae of the genu of the pedipalp and of the dorsal seta of the chelicera. The form of the sclerotized structures of the endogynium is characteristic for the females.

The seven British species which I have assigned to this subgenus are keyed below.

Subgenus ***Paragamasus*** Hull, 1918
(including *Leptogamasus* Trägårdh)
Type: ***Pergamasus robustus*** (Oudemans, 1902)

The majority of the British species of *Pergamasus* fall into this subgenus. There are never more than thirty-five pairs of setae on the opisthonotal region of the dorsal shield and the setae of the opisthogastric shield in the female number eight, nine or ten (excluding the three setae associated with the anus). The species range in length from 400–1,200μ. The dorsal shield in the male often shows an incomplete fusion of the podonotal and opisthonotal elements ; their juncture being indicated by a transverse suture. The tectum is basically three-pronged throughout. The separation of the males has been made largely on the armature of leg II, the form and chaetotaxy of the trochanter of the pedipalp, the shape and dentition of the chelicera and the chaetotaxy of the dorsum. The females show greater morphological homogeneity and although it has been possible to divide them into groups on the basis of such characters as the fusion of the peritrematal shield with the opisthogastric shield, the number of setae on the opisthogastric shield and the chaetotaxy of the dorsal shield, specific diagnosis in a number of cases depends on the form of the genital shield and the endogynial processes. The characters associated with the genital shield and endogynium are so difficult to define for key purposes that for identification purposes it will be necessary to remove the genital shield and compare its structure with the illustrations.

KEY TO ADULTS OF THE BRITISH MITES OF THE GENUS *Pergamasus* BERL. S. LAT.

MALES

1 Opisthonotal region with a dense covering of setae, more than 45 pairs (Text-fig. 82) (Subgenus ***Pergamasus***) 2

– Opisthonotal region with a moderate covering of setae, not more than 35 pairs (Text-fig. 152) . . . . (Subgenus ***Paragamasus***) 7

2 Chaetotaxy of the podonotal region displaying neotrichy, more than 45 pairs of setae present (Text-fig. 82) ; femur II with two spurs (Plate 2c) ; dorsal shield with a distinct transverse suture indicating the juncture of the podonotal and opisthonotal shields . . . . . ***P. (Pergamasus) hamatus*** (Koch) (p. 169)

– Chaetotaxy of the podonotal region not displaying neotrichy, 25–27 pairs of setae present (Text-fig. 76) ; femur II with at the most a single spur (Plate 1a) . . 3

3 Dorsum with a transverse suture (Text-fig. 76) ; coxa II with processes (Plate 2a) ; tibia II unarmed (Plate 2b) ; prae-endopodal shields almost meeting in the mid-line ; genital lamina weakly developed . ***P. (Pergamasus) mirabilis*** Willmann (p. 166)

– Dorsum without a transverse suture (Text-fig. 50) ; coxa II unarmed ; tibia II armed with one or more spur-like processes ; prae-endopodal shields widely separated 4

4 Internal setae of the genu of the pedipalp spatulate, entire ; tibia of leg II with a large ventro-lateral process (Plate 1b) ; dorsal seta of the chelicera simple . 5

– Internal setae of the genu of the pedipalp denticulate distally (Text-fig. 64) ; tibia II without such large process (Plate 1e) ; dorsal seta of the chelicera denticulate distally (Text-fig. 65) 6

5 Ventro-lateral process of tibia II hook-like distally (Plate 1b) ***P. (Pergamasus) longicornis*** Berlese (p. 155)

– Ventro-lateral process of tibia II rounded distally (Plate 1a) ***P. (Pergamasus) crassipes*** (L) Berlese (p. 151)

6 Genu II strongly spurred (Plate 1c) ; femur II without spur ; genital lamina produced into a median spine (Text-fig. 51) ***P. (Pergamasus) septentrionalis*** (Oudemans) (p. 159)

– Genu II unarmed (Plate 1d) ; femur II with a truncated spur ; genital lamina may be medially incised (Text-fig. 62) ***P. (Pergamasus) quisquiliarum*** (Canestrini) (p. 163)

7 Dorsum entire, without transverse suture (Text-fig. 235) 8

– Dorsum with a transverse suture (Text-fig. 239) 13

8 Coxa and trochanter of leg II tuberculated (Plate 2e & f) ; movable digit of the chelicera bidentate (Text-fig. 113), fixed digit truncate distally ; with scale-like elevations near sternal setae V (Text-fig. 110) ***P. (Paragamasus) alpestris*** Berlese (p. 178)

– Coxa and trochanter of leg II not tuberculated ; movable digit of the chelicera uni- or bidentate, fixed digit rounded distally (Text-fig. 251) without scale-like elevations near sternal setae V 9

9 Dorsal shield greater than 700μ in length 10

– Dorsal shield less than 500μ in length 11

10 Dorsal seta R5 about twice the length of S4 (Text-fig. 203) : spur on tibia II in the form of a ridge (Plate 4e) . . ***P. (Paragamasus) leruthi*** Cooreman (p. 204)

– Dorsal setae R5 and S4 subequal in length (Text-fig. 181) ; spur on tibia II digitiform (Plate 4b) . . . . . . ***P. (Paragamasus) integer*** sp. nov. (p. 197)

11 Fixed digits of the chelicera tapering distally, not hooked ; movable digit unidentate (Text-fig. 282) . . . . . ***P. (Paragamasus) suecicus*** (Trägårdh) (p. 228)

– Fixed digit of chelicera hooked distally ; movable digit bidentate (Text-fig. 251) . 12

12 Spurs on femur II minute, main spur scarcely longer than the accessory spur (Plate 5b) . . . . **P. (Paragamasus) nathistmus** sp. nov. (p. 214)
– Spurs on femur II larger, main spur about twice the length of the accessory spur (Plate 5f) . . . . . **P. (Paragamasus) rothamstedensis** sp. nov. (p. 219)

13 Corniculus with triangular hyaline appendage (Text-fig. 167) ; genu II unarmed (Plate 3b) . . . . . . **P. (Paragamasus) diversus** Halbert (p. 192)
– Corniculus without such appendage ; genu II armed with a spur 14

14 Trochanter of pedipalp without seta-bearing tubercle (Text-fig. 99) 15
– Trochanter of pedipalp with a strong seta-bearing proximal tubercle (Text-fig. 195) 16

15 Trochanter II spurred (Plate 2d) . **P. (Paragamasus) robustus** (Oudemans) (p. 174)
– Trochanter II not spurred ; leg II figured (Plate 6d) **P. (Paragamasus) truncus** Schweizer (p. 234)

16 Sternal seta V arising from a scale-like elevation (Text-fig. 193) 17
– Sternal seta V not arising from a scale-like elevation 18

17 Trochanter II with a strong spur-like projection (Plate 4c) ; leg II (Plate 4d) ; trochanter IV with process (Text-fig. 197) **P. (Paragamasus) lapponicus** Trägårdh (p. 200)
– Trochanter II without such projection ; leg II (Plate 6c) ; trochanter IV without process . . . . . **P. (Paragamasus) teutonicus** Willmann (p. 231)

18 Femur II with a conspicuous tubercle proximal to the lyriform fissure (Plate 4a) ; anterior rows of deutosternal denticles strongly arched (Text-fig. 180) ; leg II figured (Plate 4a) . . . . **P. (Paragamasus) femoratus** sp. nov. (p. 197)
– Femur II without tubercle proximal to lyriform fissure 19

19 Dorsal shield 500μ or less in length ; main spur on femur II considerably shorter than the length of tibia II (Plate 6d) 20
– Dorsal shield 700μ or greater in length ; main spur on femur II about equal in length to or longer than tibia II (Plate 3g) 22

20 Femur II with a strong sclerotized ridge proximal to the main spur (Plate 6e) ; spur on tibia slender . . **P. (Paragamasus) wasmanni** (Oudemans) (p. 237)
– Femur II without sclerotized ridge proximal to the main spur (Plate 5a) ; spur on tibia II broad 21

21 Proximal seta on the trochanter of the pedipalp about equal to the height of the tubercle (Text-fig. 138) ; leg II (Plate 3a) **P. (Paragamasus) cambriensis** sp. nov. (p. 186)
– Length of the proximal seta on the trochanter of the pedipalp about twice the height of the tubercle (Text-fig. 227) ; leg II (Plate 5a) **P. (Paragamasus) misellus** Berlese (p. 211)

22 Accessory spur on femur II broad, truncate (Plate 5c) 23
– Accessory spur on femur II slender, tapering distally (Plate 6a) 25

23 Main spur on femur II slender without tubercle (Plate 3d) ; trochanter II with sclerotized process distally (Plate 3c) ; leg II (Plate 3d) **P. (Paragamasus) cassiteridum** sp. nov. (p. 188)
– Main spur on femur II with distinct tubercle (Plate 5g) ; trochanter II without sclerotized process distally 24

24 Trochanter of pedipalp with a distinct tubercle proximal to the seta-bearing tubercle (Text-fig. 242) ; leg II (Plate 5c) . **P. (Paragamasus) parrunciger** sp. nov. (p. 216)
– Trochanter of pedipalp without tubercle proximal to the seta-bearing tubercle (Text-fig. 261) ; leg II (Plate 5g) . **P. (Paragamus) runciger** (Berlese) (p. 222)

25 Fixed digit of the chelicera markedly broad anterior to the lyriform fissure (Text-fig. 156) ; leg II (Plate 3g) . . . **P. (Paragamasus) celticus** sp. nov. (p. 192)
– Fixed digit of the chelicera relatively slender (Text-fig. 131) ; leg II (Plate 2g) . 26

26 Trochanter of pedipalp with a distinct tubercle proximal to the seta-bearing tubercle (Text-fig. 270) ; spurs on leg II as in Plate 6a **P. (Paragamasus) schweizeri** sp. nov. (p. 225)

– Trochanter of pedipalp without tubercle proximal to the seta-bearing tubercle (Text-fig. 130) ; spurs on leg II as in Plate 2g **P. (Paragamasus) armatus** Halbert (p. 183)

FEMALES

1 Opisthonotal region of dorsal shield with a moderate covering of setae, never more than 35 pairs (Text-fig. 134) ; peritrematal shield free posteriorly or fused with the opisthogastric shield (Text-figs. 141 & 123) ; opisthogastric shield with a maximum of ten pairs of setae, excluding the three setae associated with the anus . . . . (Subgenus **Paragamasus**) 7

– Opisthonotal region of dorsal shield with a dense covering of setae, more than 45 pairs (Text-fig. 55) ; peritrematal shield fused with the dorsal shield along its entire length or free in its posterior half (Text-figs. 47 & 93) ; opisthogastric shield with never less than 14 pairs of setae (Text-fig. 47) (Subgenus **Pergamasus**) 2

2 Podonotal region of the dorsal shield neotrichous with more than 35 pairs of setae (Text-fig. 88) ; peritrematal shield free in its posterior half (Text-fig. 24) ; tectum three-pronged (Text-fig. 90) . **P. (Pergamasus) hamatus** (Koch) (p. 169)

– Podonotal region of the dorsal shield with never more than 25 pairs of setae (Text-fig. 35) ; peritrematal shield fused with the dorsal shield along its entire length or free in its posterior half (Text-figs. 36 & 93) ; tectum basically three- or five-pronged (Text-figs. 95 & 72) 3

3 Tectum basically three-pronged (Text-fig. 95), peritrematal shield free in its posterior half (Text-fig. 93) ; endogynium characteristic (Text-fig. 94) ; dorsal shield 1,200μ in length . . . . . **P. (Pergamasus) hortensis** sp. nov. (p. 173)

– Tectum basically five-pronged (Text-fig. 38) ; peritrematal shield fused with the dorsal shield along its entire length ; large species, greater than 1,200μ in length 4

4 Endogynium with a pair of large horn-like structures (Text-fig. 56) ; no reticulated endogynial sacs ; trochanter IV with a sclerotized protuberance (Text-fig. 60) **P. (Pergamasus) septentrionalis** (Oudemans) (p. 159)

– Endogynium without paired horn-like structure but with a pair of reticulated sacs separated by a median process (Text-fig. 70) ; trochanter IV without sclerotized protuberance 5

5 Internal setae of the genu of the pedipalp denticulate distally (Text-fig. 74) ; dorsal seta of the chelicera denticulate distally (Text-fig. 73) ; opisthogastric shield with twenty or more pairs of setae excluding the anals (Text-fig. 68) **P. (Pergamasus) quisquiliarum** (Can.) (p. 163)

– Internal setae of the genu of the pedipalp spatulate ; entire dorsal seta of the chelicera simple (Text-fig. 49) ; opisthogastric shield with about 15 pairs of setae (Text-fig. 36) 6

6 Median process of endogynium strongly bifurcate distally (Text-fig. 47) ; genital shield as in Plate 7b . . . . **P. (Pergamasus) longicornis** Berl. (p. 155)

– Median process of endogynium entire (Text-fig. 37) ; genital shield as in Plate 7a **P. (Pergamasus) crassipes** (L) Berl. (p. 151)

7 Peritrematal shield fused with the opisthogastric shield posteriorly (Text-fig. 284) ; with 9 pairs of opisthogastric setae (Text-fig. 284) 8

– Peritrematal shield free posteriorly (Text-fig. 25) ; with 8 or 10 pairs of opisthogastric setae (Text-figs. 254 & 275) 10

8 Genital shield rounded anteriorly (Plate 7l) **P. (Paragamasus) suecicus** Trägårdh (p. 228)

– Genital shield triangular anteriorly (Plate 7g) . . . .

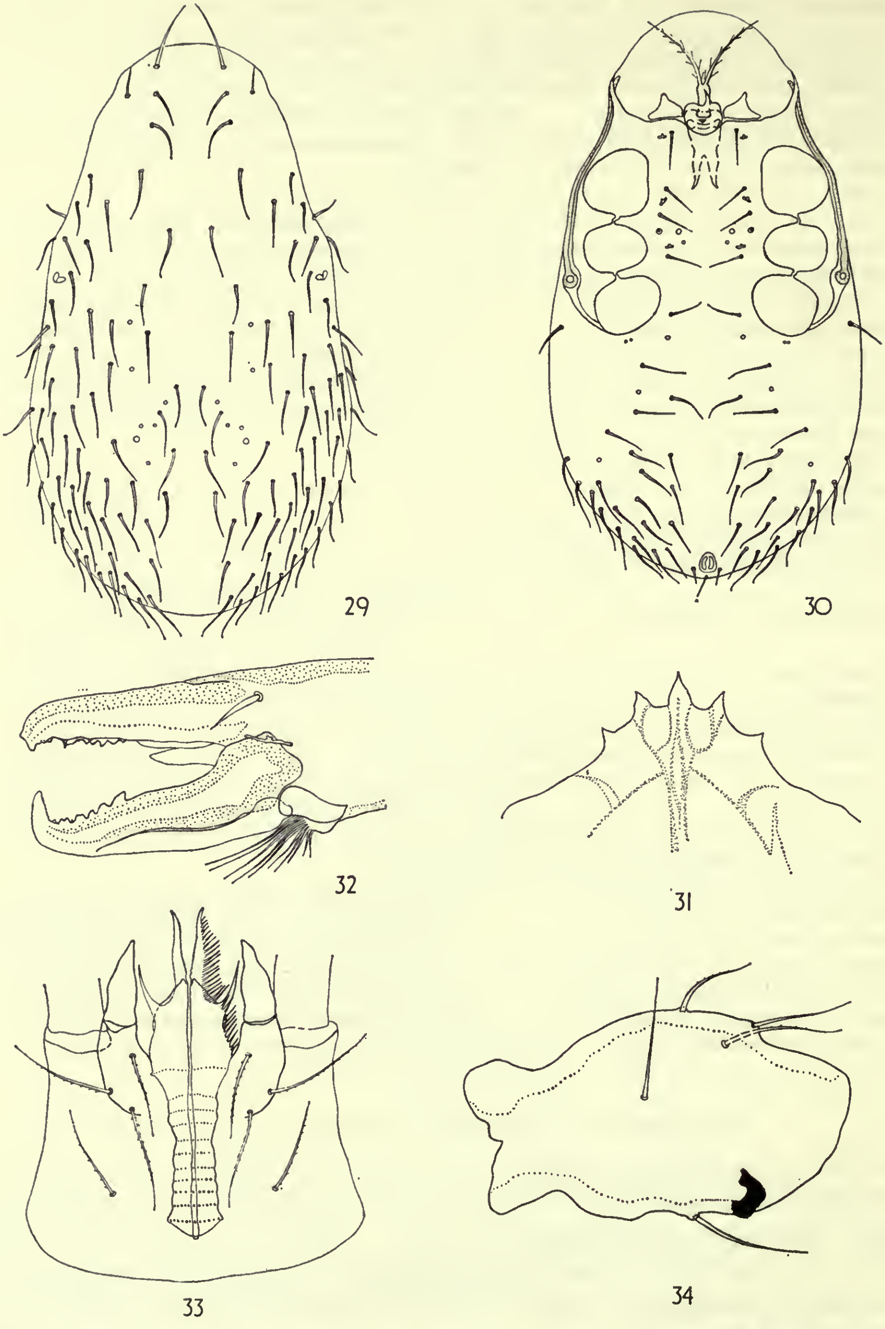
9 Endogynial processes as in Text-fig. 210 **P. (Paragamasus) leruthi** Cooreman (p. 204)
– Endogynial processes as in Text-fig. 124 . **P. (Paragamasus) alstoni** sp. nov. (p. 181)
10 Opisthogastric shield with 8 pairs of setae excluding anals (Text-fig. 254) . . 11
– Opisthogastric shield with 10 pairs of setae excluding anals (Text-fig. 188) . . 12
11 Genital shield as in Plate 7k . **P. (Paragamasus) rothamstedensis** sp. nov. (p. 219)
– Genital shield as in Plate 7j . . **P. (Paragamasus) londonensis** sp. nov. (p. 207)
12 Dorsal setae R5 and S4 subequal in length (Text-fig. 187) ; genital shield and endogynial processes as in Plate 7i and Text-fig. 189 respectively **P. (Paragamasus) integer** sp. nov. (p. 197)
– Dorsal seta R5 considerably longer than S4 (Text-figs. 231 & 302) . . . 13
13 Small species 450–550μ in length ; peritreme extending to the middle of coxa II ;
Genital shield as in Plate 8a . . **P. (Paragamasus) misellus** Berlese (p. 211)
Genital shield as in Plate 8e . **P. (Paragamasus) wasmanni** (Oudemans) (p. 237)
Genital shield as in Plate 8b . . **P. (Paragamasus) truncus** Schweizer (p. 234)
Sterniti-genital region as in Text-fig. 222 **P. (Paragamasus) minimus** sp. nov. (p. 211)
Genital shield as in Plate 8d . . **P. (Paragamasus) cambriensis** sp. nov. (p. 186)
– Large species 700–1,200μ in length ; peritreme usually extending beyond coxa II . 14
14 Large species, dorsal shield 1,100–1,200μ in length 15
– Smaller species, dorsal shield usually 700–800μ in length (except **P. (Paragamasus) longisetosus**, 975–1,000μ) 16
15 Endogynial processes and genital shield as in Text-fig. 104 and Plate 7e respectively ; peritreme extending to the middle of coxa II **P. (Paragamasus) robustus** (Oudemans) (p. 174)
– Endogynial processes and genital shield as in Text-fig. 118 and Plate 7f respectively **P. (Paragamasus) alpestris** Berlese (p. 178)
16 Dorsal setae conspicuously long and thick (Text-fig. 216) ; species 975–1,000μ in length . . . . . **P. (Paragamasus) longisetosus** sp. nov. (p. 207)
– Dorsal setae relatively shorter and never thickened ; less than 900μ in length . 17
17 Posterior incision of the sternal shield extending to the level of sternal setae II (Text-fig. 170) ; genital shield with an anterior arrow-like sclerotized area (Plate 7h) **P. (Paragamasus) diversus** Halbert (p. 192)
– Posterior incision of the sternal shield never reaching the level of sternal setae II ; genital shield without such sclerotized area
a Genital shield as in Plate 8k . . . **P. (Paragamasus) runciger** Berlese(p. 222)
b Genital shield as in Plate 8j . . **P. (Paragamasus) parrunciger** sp. nov. (p. 216)
c Genital shield as in Plate 8c . . . **P. (Paragamasus) armatus** Halbert (p. 183)
d Genital shield as in Plate 8h & i . **P. (Paragamasus) lapponicus** Träg. (p. 200)
e Genital shield as in Plate 8m & n . **P. (Paragamasus) teutonicus** Willmann (p. 231)
f Genital shield as in Plate 8f & g . . **P. (Paragamasus) celticus** sp. nov. (p. 192)
g Genital shield as in Plate 8l . . **P. (Paragamasus) schweizeri** sp. nov. (p. 225)

Pergamasus (Pergamasus) crassipes (L) Berlese

Gamasus (*Pergamasus*) *crassipes :* Berlese A (1906) *Redia* **3** : 229 (male only).
Gamasus (*Pergamasus*) *crassipes var. longicornis* Berlese (1906) *Redia* **3** : 232 (female only).

MALE. The male is ruddy brown in colour. The dorsal shield (1,268–1,383μ in length × 747–864μ wide) is pear-shaped, regionally reticulated, strongly sclerotized and without a transverse suture. The opisthosomal region is densely covered with setae (Text-fig. 29).

Ventrally, there are two large prae-endopodal shields flanking the genital sclerite. The tritosternum has a pair of well developed pilose laciniae. About half of the



Figs. 29–34. *Pergamasus* (*Pergamasus*) *crassipes* (L.) Berlese, male.
Fig. 29 dorsum of idiosoma. Fig. 30 venter. Fig. 31 tectum. Fig. 32 chelicera. Fig. 33 venter of gnathosoma. Fig. 34 trochanter of leg IV.

tritosternum is covered by the genital lamina. The genital lamina is produced anteriorly into a sharply pointed spine. The arrangement of the sternal setae and pores are shown in Text-fig. 30.

The stigma is situated ventro-laterally between coxae III and IV ; the peritreme extends to coxa I. The post-stigmatal extension of the peritrematal shield reaches the posterior region of coxa IV. A pair of post-stigmatal setae is present.

The tectum is produced anteriorly into five short tooth-like processes (Text-fig. 31). The most distinctive features of the chaetotaxy of the pedipalp are, the comb-like seta on the femur and the spatulate setae on the genu. The palpal trochanter is without a tubercle. The chelicera is strong with a simple dorsal seta. The fixed digit is truncated. Both digits possess rows of teeth (Text-fig. 32). The spermadactyl is normal. The corniculus is distinctly stalked. The entire lateral (outer) margins of the hypostomal processes are fringed (Text-fig. 33). The hypostomal setae are pilose. The deutosternal teeth of the ventral groove are arranged in eleven transverse rows.

The tarsus (333–360μ) of leg I is longer than the tibia (254–266μ). The praetarsus is 19–25μ long. The femur of leg II is crassate with a strong falcate spur. The terminal end of the main process of the tibia is almost rounded and its distal spur is shown in Plate 1a. The trochanter of leg II is shown in Text-fig. 34.

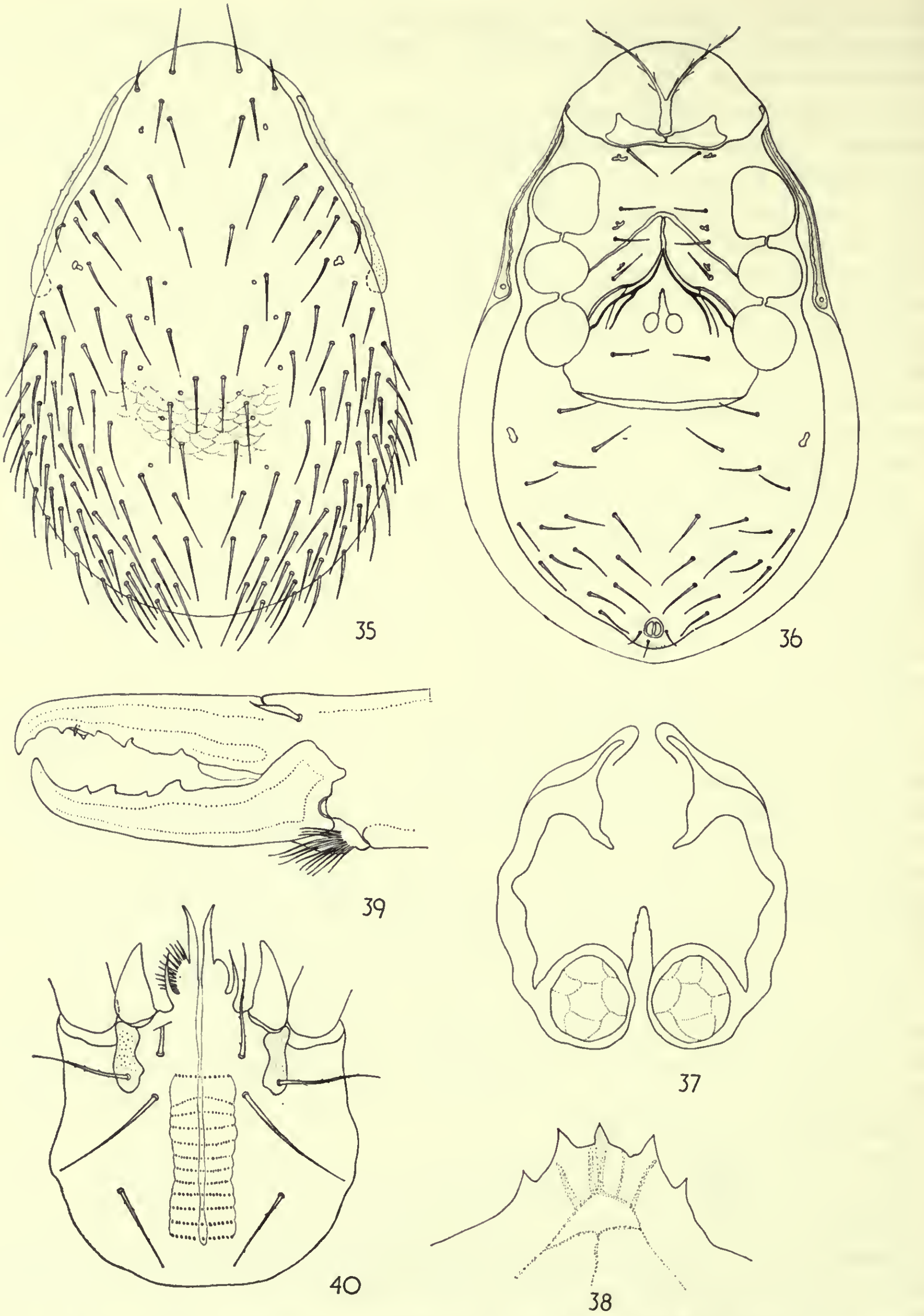
FEMALE. The dorsum of the dark brown, strongly sclerotized idiosoma is neotrichous (Text-fig. 35). The dorsal shield (1,200–1,351μ long × 782–917μ wide) is oval and regionally reticulated.

The tritosternum is well developed with a pair of pilose laciniae. There is a pair of prae-endopodal shields almost meeting in the medial line (Text-fig. 36). The metasternal shields are free. The endogynium is furnished with a pair of round faintly reticulated sacs with a short median process arising between them (Text-fig. 37). The terminal end of the process may be smooth or slightly serrated. The genital shield is shown in Plate 7a. The opisthogastric shield usually has fifteen pairs of setae of variable length (excluding the three setae associated with the anus). Ventrally the stigma is situated a little behind coxa III and the peritreme extends to coxa I. The peritrematal shield is fused with the dorsal shield.

The tectum is five-pronged (Text-fig. 38). The pedipalp is essentially the same as in the male. The dentition of the fixed digit is well shown in Text-fig. 39. Fringes are confined to the proximal portion of the hypostomal processes (Text-fig. 40). The deutosternal denticles are arranged in twelve transverse rows. The gnathosomal setae are distinctly pilose.

Leg I has the tarsus (342–404μ) longer than the tibia (241–291μ) ; the praetarsus is 25–29μ long. The trochanter of leg IV is without a process.

DISTRIBUTION AND HABITAT. I have examined material from : In litter under *Cupressus* sp. (Rothamsted Lodge, Rothamsted Experimental Station, Harpenden, Hertfordshire, G. Owen Evans and E. Browning, 18.iii.1957). In leaf mould (Forest of Dean, Gloucestershire, J. T. Salmon, 27.ix.1951). Oak and birch leaves (Newton Abbot, S. Devon, R. G. Lewesther, 21.vi.1951). Litter and humus under pines and holly (summit of Dove Crag, near Ambleside, Westmorland, M. E. Bacchus,



Figs. 35–40. *Pergamasus* (*Pergamasus*) *crassipes* (L.) Berlese, female.
Fig. 35 dorsum of idiosoma. Fig. 36 venter. Fig. 37 endogynial process. Fig. 38 tectum.
Fig. 39 chelicera. Fig. 40 venter of gnathosoma.

28.ii.1954). *Sphagnum*, etc. (Cock Hill, Yorkshire, J. T. Salmon, 21.vii.1951). In leaf mould (Epping Forest, Essex, J. T. Salmon, 27.v.1951). In leaf mould (Savernake Forest, Berkshire, J. T. Salmon, 26.ix.1951). In moss of wall (Tarn Hows, North Lancashire, M. E. Bacchus, 4.xii.1954). In moss (Grassington, Grass Woods, North Riding, Yorkshire, J. T. Salmon, 24.vi.1951). *Sphagnum* (Ascot, Berkshire, A. H. G. Alston, 8.xii.1957). Leaf litter from woods (near Buxton, Derbyshire, J. T. Salmon, 23.vi.1951). Moss on tree stumps and stones (Forest of Dean, Gloucestershire, J. T. Salmon, 27.ix.1951). In beech leaf mould from steep bank (Rickmansworth, Hertfordshire, M. E. Bacchus, 25.ii.1951). In leaf mould (Richmond Park, Surrey, J. T. Salmon, 19.iii.1951). In leaf mould (Burnham Beeches, Buckinghamshire, J. T. Salmon, 3.vi.1951). (Roy. Bot. Gdns., Kew, Surrey, J. L. Gilbert, —.iii.1961). Moss, humus, hollow tree (Swansea University, Swansea, P. N. Lawrence, 26.iii.1962). *Sphagnum*, etc. (Moel Siabod, North Wales, P. N. Lawrence, 22.x.1960). In moss (Tarbert, Crianlarich, Loch Lomond, Dunbarton, J. T. Salmon, 3.vii.1951). In dead leaves (Loch Lomond between Glasgow and Tarbert, Dunbarton, J. T. Salmon, 8.vii.1951).

Biological notes. Eggs from four females kept under laboratory conditions hatched within one to three days (average 2·16 days) of deposition. The eggs are densely covered with hair-like outgrowths. The larva is sluggish and does not feed. It moults in one to eight days (average 3·16) into an active feeding protonymph. The protonymphal stage lasts nine to thirteen days (average 10·0). The deutonymph is also active and feeding lasts seven to thirty-five days (average 24·22). Unlike *P.* (*P.*) *robustus*, males and females were reared from the egg batch laid by each female.

There is considerable confusion in the literature concerning the identity of *P.* (*P.*) *crassipes*. Berlese (1906) in his monograph describes and figures two forms, namely, *Gamasus* (*Pergamasus*) *crassipes* (L.) and *G.* (*P.*) *crassipes* var. *longicornis* Berlese. These two forms are readily distinguishable by the armature of the tibia of leg II in the male. Unfortunately, Berlese connected the wrong female and male; thus the female of *G.* (*P.*) *crassipes* : Berlese is really the female of *G.* (*P.*) *crassipes* var. *longicornis* Berlese. I have verified this by examining material in the Berlese Collection at Florence and by rearing *P.* (*P.*) *crassipes* in the laboratory. I consider the two " forms " to be distinct sympatric species which can be distinguished by a number of morphological characters. Owing to the confusion regarding the identity of these species, I have not attempted a full synonymy.

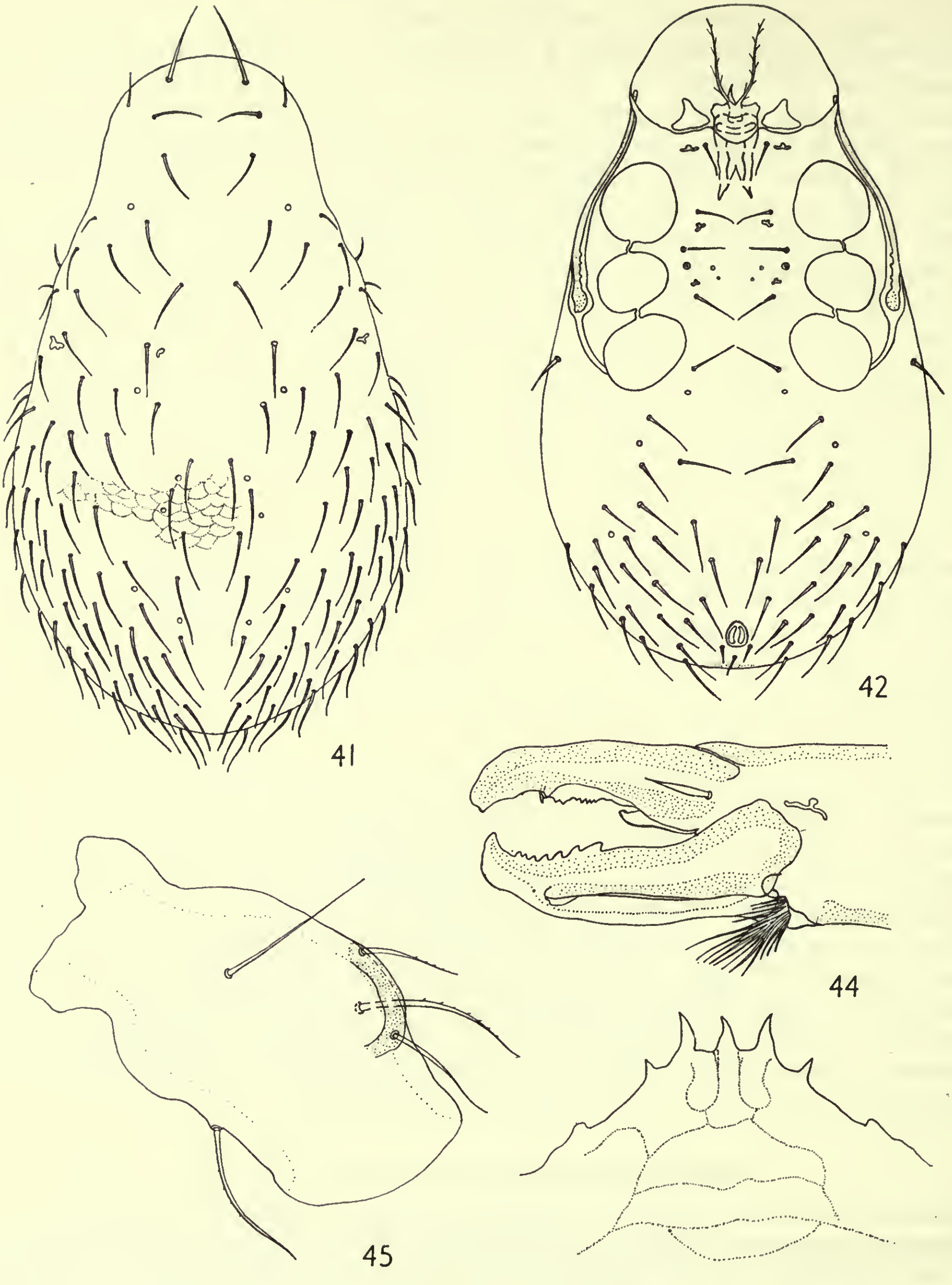
Pergamasus (Pergamasus) longicornis Berlese

Gamasus (*Pergamasus*) *crassipes* var. *longicornis* Berlese, A. (1906). *Redia* **3** : 232, fig.

Gamasus (*Pergamasus*) *crassipes* (L.) Latr. Berlese, A. (1906). *Redia* **3** : 229, fig. (female only).

Pergamasus crassipes (L.) var. *longicornis* : Trägårdh, I. (1912), *Arch. Zool. Expér. gén.* **8** : 523, figs. ; Trägårdh, I. (1931). *The Natural History of Juan Fernandez and Easter Islands* **3** : 603, figs. ; Turk, F. A. (1945). *Ann. Mag. nat. Hist.* **12** 11 : 802, figs. ; Schweizer, J. (1961). *Denks. schweiz. naturf. Ges.* **84** : 59, figs.

Gamasus (*Pergamasus*) *crassipes* (L.) var. *longicornis* : Halbert, J. N. (1915). *Proc. R. Irish Acad.* **31** 39 ii : 54, fig.



FIGS. 41–45. *Pergamasus* (*Pergamasus*) *longicornis* Berlese, male.
Fig. 41 dorsum of idiosoma. Fig. 42 venter. Fig. 43 tectum. Fig. 44 chelicera. Fig. 45 trochanter of leg IV.

Pergamasus crassipes (L.) Latr. var. *longicornis :* Womersley, H. (1942). *Trans. Roy. Soc. S. Aust.* **66** (2) : 146, figs. (male only).

Pergamasus crassipes longicornis : Cooreman, J. (1943). *Bull. Mus. nat. Bel.,* **19** 63 : 4, fig.

Amblygamasus septentrionalis belgicus Cooreman, J. (1943). *Bull. Mus. nat. Bel.,* **19** 63 : 4, figs.

MALE. The dorsal shield (1,275–1,284μ long × 714–747μ wide) is pear-shaped and strongly sclerotized. The opisthonotal shield is densely covered with setae (Text-fig. 41).

The tritosternum is provided with a pair of pilose laciniae. The genital lamina is anteriorly produced into a sharp median spine (Text-fig. 42). A pair of prae-endopodal shields is present. The stigma is situated between coxae III and IV ; the peritreme extends to coxa I. There is a post-stigmatal prolongation of the peritrematal shield which reaches to coxa IV. A pair of post-stigmatal setae is present.

The tectum has five prongs (Text-fig. 43). The most distinctive features of the pedipalp are : the trochanter without any tubercle, the femur with a comb-like seta and the genu with two spatulate setae. The chelicera is robust and shown in Text-fig. 44. The corniculus and hypostomal processes are similar to those in *P. crassipes*.

The tibia, tarsus and prae-tarsus of leg I are 250–266μ, 304–342μ and 25–35μ long respectively. Leg II : the femur is crassate with a strong falcate spur and the genu has a tubular spur ; the tibia has three spurs, namely distal, medial and lateral (Plate 1b). The median process terminates in a hook-like structure, and this shape is constant in all the specimens I have examined. The distinctive shape of the trochanter of leg IV is figured (Text-fig. 45).

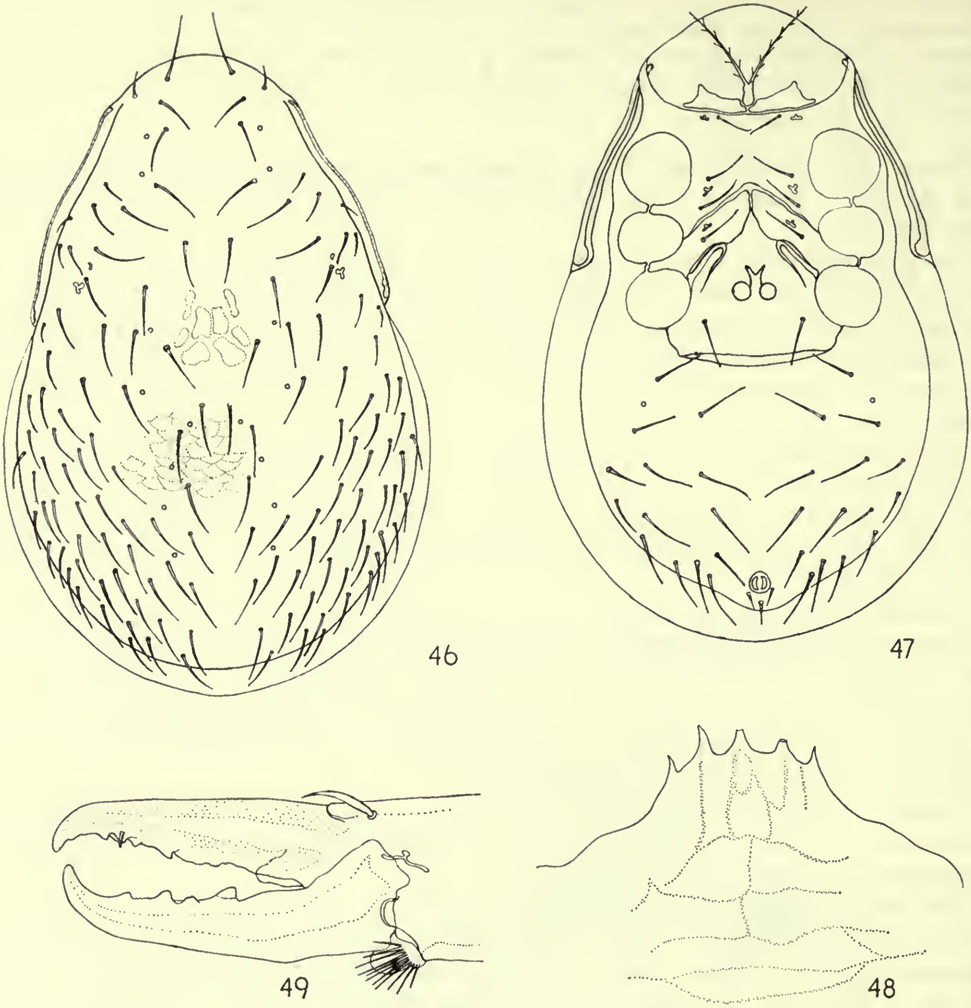
FEMALE. The dorsal shield measures 1,268–1,317μ long × 797–815μ wide and is dark brown to deep yellow in colour. The distribution and relative lengths of the dorsal setae are shown in Text-fig. 46.

The tritosternum and prae-endopodal shields are delineated as in Text-fig. 47. The metasternal shields are free. The endogynium has a pair of round sacs with a bifurcate median process. Each sac is strongly reticulated. The genital shield is shown in Plate 7b. The setation of the opisthogastral shield is shown in Text-fig. 47. The stigma is situated between coxae III and IV with the peritreme extending to coxa I. The peritrematal shield is entirely fused with the dorsal shield.

The tectum is five-pronged (Text-fig. 48). The pedipalp is essentially similar to that in the male. The chelicera is figured (Text-fig. 49).

Leg I has the tibia, tarsus and prae-tarsus 262–266μ, 358–363μ and 29–35μ long respectively. The trochanter of leg IV lacks a spur.

DISTRIBUTION AND HABITAT. This species has been recorded from Northern Europe (Berlese, 1906), Germany, Norway (Trägårdh, 1912), Ireland (Halbert, 1915), Juan Fernandez and Easter Islands (Trägårdh, 1931), Australia (Womersley, 1942) and Belgium (Cooreman, 1943). I have examined specimens from litter under *Cupressus* sp. (Rothamsted Lodge, Rothamsted Experimental Station, Harpenden, Hertfordshire, G. Owen Evans and E. Browning, 18.iii.1957). Oak and birch leaves



Figs. 46–49. *Pergamasus* (*Pergamasus*) *longicornis* Berlese, female. Fig. 46 dorsum of idiosoma. Fig. 47 venter. Fig. 48 tectum. Fig. 49 chelicera.

(Newton Abbot, S. Devon, R. G. Lewesther, 21.vi.1951). Litter and humus under pines and holly (Duddleswell, Ashdown Forest, Sussex, K. H. Hyatt, 10.ix.1956). Moss leaves (Adelaide Hill, Bowness, Cumberland, J. T. Salmon, 29.vi.1951). Summit of Dove Crag, 2,600 ft. (near Ambleside, Westmorland, M. E. Bacchus, 28.ii.1954). *Sphagnum*, etc. (Cock Hill, Yorkshire, J. T. Salmon, 21.vii.1951). In leaf mould (Epping Forest, Essex, J. T. Salmon, 27.v.1951). In leaf mould (Savernake Forest, Berkshire, J. T. Salmon, 26.ix.1951). In moss of wall (Tarn Hows, N. Lancashire, M. E. Bacchus, 4.xii.1954). Litter under thick evergreen hedge (St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 29.iii.1957). Litter and soil under evergreen trees (St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 5.iv.1957). (Royal Botanical Gardens, Kew, Surrey, J. L. Gilbert, 5.iii.1961). Moss from crevices in rocks (near Force Forge, Westmorland, M. E. Bacchus, 2.xii.1954). In oak and beech leaf mould (Grasmere, Westmorland, J. T. Salmon, 26.vi.1951). Moles' (*Talpa europaea*) nest, near pasture (Godstow, Berkshire, Prof. P. A. Larkin, 4.ii.1962). Rotten black leaves at riverside rocks (on the river Brathy, S.W. Ambleside, Lancashire, P. N. Lawrence, 23.ix.1956).

From pine litter (Clyne Park, Swansea, S. K. Bhattacharyya, 4.i.1961). Salt marsh debris, (Llanrhidian, Glamorgan, P. N. Lawrence, 27.iii.1962). Yew and rhododendron humus (Educational Garden, Swansea University, Swansea, P. N. Lawrence, 26.iii.1962).

In moss (Tarbert, Crianlarich, Loch Lomond, Dunbarton, J. T. Salmon, 3.vii.1951). In moss and heather (Glen Garry, Perth, J. T. Salmon, 5.vii.1951). In dead leaves (Loch Lomond, between Glasgow and Tarbert, J. T. Salmon, 8.vii.1951).

Moss on rock (Caherbannagh, Co. Clare, Ireland, Nottingham University Expedition, viii.1961).

Pergamasus (Pergamasus) septentrionalis (Oudemans)

Parasitus septentrionalis Oudemans, A. C. (1902). *Tijdschr. Ent.* **45** : 39, figs.

Gamasus (*Amblygamasus*) *septentrionalis* : Berlese, A. (1906). *Redia* **3** : 188, figs.

Gamasus (*Amblygamasus*) *septentrionalis* var. *norvegicus* Berlese, A. (1906). *Redia* **3** : 190, figs. ; Sellnick, M. (1940). *Göteborgs VetenskSamh. Handl.* (5) **68** 14 : 58, figs.

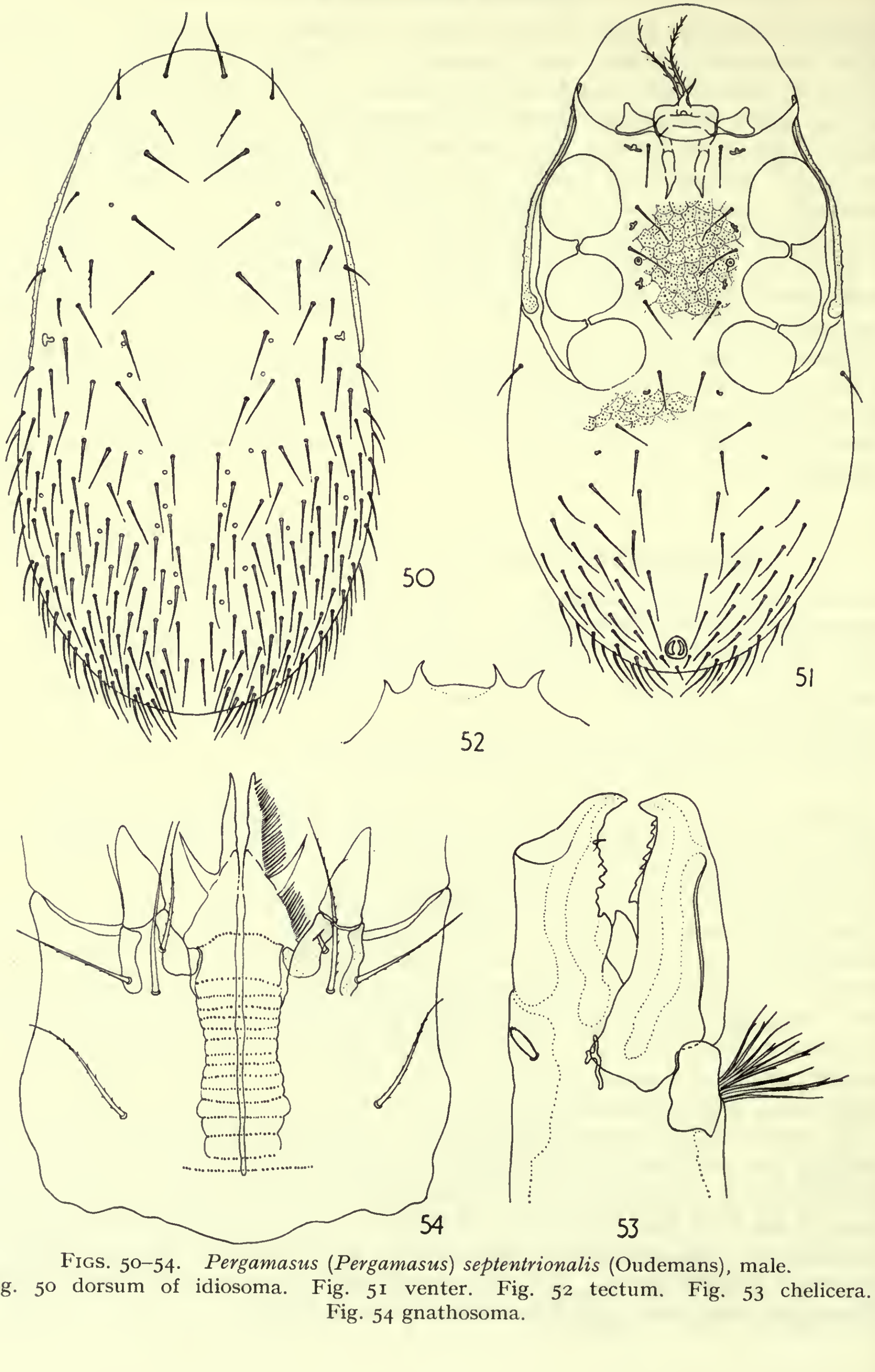
Amblygamasus septentrionalis (Oudemans) 1902. Haarlov, N. (1957). *Spolia zool. Mus. Hauniensis* **17** : 16, figs.

Amblygamasus septentrionalis (Oudemans) *norvegicus* Berlese 1905. Halašková, V. (1959). *Zvlástni. Otisk Mus. Zprávy Pražského Kraje* **4** : 6, figs.

MALE. This species is strongly sclerotized and reddish-brown in colour. The dorsal shield (1,383–1,463μ long × 714–721μ wide) is regionally reticulated. Only the opisthonotal shield is densely covered with setae (Text-fig. 50). Some dorsal shield setae appear to be pilose under high magnification.

The tritosternum has a pair of pilose laciniae. The genital lamina is produced, anteriorly, into a well developed sharp, median spine (Text-fig. 51). There is a pair of prae-endopodal shields. The sternal setae are sparsely pilose under high magnification. The pitted reticulation extends from the anterior margin of the sternal shield to a little behind coxae IV. The stigma is situated between coxae III and IV ; and the peritreme extends as far as coxa I. The post-stigmatal extension of the peritrematal shield extends to coxa IV.

The tectum is four-pronged (Text-fig. 52). The most distinctive features of the pedipalp are : the femur with one and the genu with two distally denticulated setae. The chelicera is robust and its digit has a row of closely-set teeth. The distinctive shape of the fixed digit is shown in Text-fig. 53 ; the dorsal seta being terminally denticulated. The corniculus is distinctively stalked and the hypostomal processes are shown in Text-fig. 54. The deutosternal denticles are arranged in fourteen or fifteen transverse rows. The hypostomal setae are pilose.



Figs. 50–54. *Pergamasus* (*Pergamasus*) *septentrionalis* (Oudemans), male. Fig. 50 dorsum of idiosoma. Fig. 51 venter. Fig. 52 tectum. Fig. 53 chelicera. Fig. 54 gnathosoma.

The tarsus (462–475μ) of leg I is considerably longer than the tibia (337–358μ) ; the prae-tarsus is 41–49μ long. Leg II ; the femur is without a distinct spur, the genu has three processes and two of them are well developed and retrogade (Plate 1c). The main tibial process is large, conical and stalked. The trochanter of leg IV is simple.

FEMALE. The dorsal shield (1,400–1,567μ long × 847–950μ wide) is strongly sclerotized and tapers anteriorly. The neotrichy is confined to the posterior half of the dorsal shield (Text-fig. 55). A few dorsal setae appear pilose under high magnification.

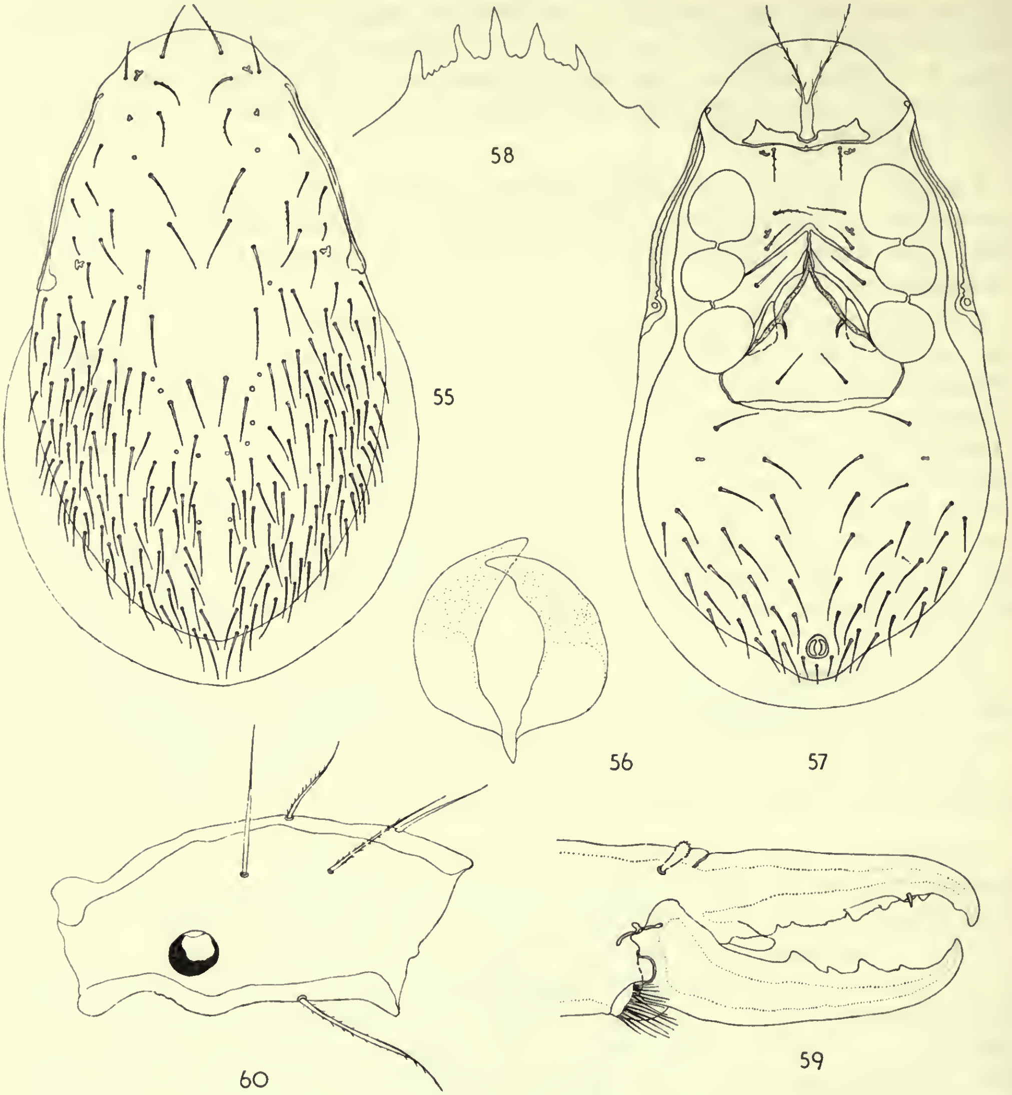
Ventrally, there are two large prae-endopodal shields almost meeting in the median line and forming a cup-shaped structure into which the base of the tritosternum is situated. The sternal setae I–III are pilose. The metasternal shields are free. The endogynium has a pair of blunt horn-like lobes joined together by a common stalk (Text-fig. 56). The genital shield is shown in Plate 7c. A very short median process may be present between the sacs. The pitted reticulation of the ventral shield extends from the anterior margin of the sternal shield to a little behind coxae IV. The distribution of setae on the opisthogastral shield is shown in Text-fig. 57. The peritrematal shield is entirely fused with the dorsal shield. The stigma is situated between coxae III and IV ; the peritreme extends to the level of coxa I.

The tectum is shown in Text-fig. 58. The pedipalp is similar to that in the male. The dentition of the chelicera and the form of the spermadactyl process are shown in Text-fig. 59. The dorsal seta of the fixed digit is terminally denticulated.

The tarsus (477–508μ) of leg I is much longer than the tibia (367–400μ) ; the prae-tarsus is 37–49μ long. The trochanter of leg IV is shown in Text-fig. 60.

DISTRIBUTION AND HABITAT. This species has already been recorded from Holland (Oudemans, 1902), Germany and Norway (Berlese, 1906), Iceland (Sellnick, 1940), Denmark (Haarlov, 1957) and Czechoslovakia (Halašková, 1959).

I have examined specimens from : leaf mould (Savernake Forest, Berkshire, J. T. Salmon, 26.ix.1951). Litter under thick evergreen hedge (St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 29.iii.1957). Rotten black leaves at riverside rocks (on the river Brathy, S.W. Ambleside, Lancashire, P. N. Lawrence, 23.ix.1956). Leaf mould from woods (near Buxton, Derbyshire, J. T. Salmon, 23.vi.1951). Rotten reeds (Colletts Bridge, nr. Wisbech, Cambridge, P. N. Lawrence). Ash humus (Colletts Bridge, nr. Wisbech, Cambridge, P. N. Lawrence, 16.x.1960). Rotten wood (Blurridge Farm, Ridge Hill, Combe Martin, Devonshire, M. E. Bacchus, 12.iii.1957). In leaf mould (Richmond Park, Surrey, J. T. Salmon, 19.iii.1951). In leaf mould (Leith Hill, Surrey, J. T. Salmon, 16.vi.1951). Summit of Dove Crag (near Ambleside, Westmorland, M. E. Bacchus, 29.ii.1954). Stratton Strawless, near Aylsham, Norwich, Norfolk, J. T. Salmon). Yew and rhododendron (Educational Garden, Swansea University, Swansea, P. N. Lawrence, 26.iii.1962). Bracken litter (Bishopston Common, Swansea, S. K. Bhattacharyya, 4.i.1961). In moss and heather (Glen Garry, Meall Doire an Daimh 1900 ft., Perth, J. T. Salmon, 5.vii.1951



FIGS. 55–60. *Pergamasus* (*Pergamasus*) *septentrionalis* (Oudemans), female. Fig. 55 dorsum of idiosoma. Fig. 56 endogynial process. Fig. 57 venter. Fig. 58 tectum. Fig. 59 chelicera. Fig. 60 trochanter of leg IV.

In moss (Tarbert, Crianlarich, Loch Lomond, Dunbarton, J. T. Salmon, 3.vii.1951). Moss on rock under Hazel (Caherbannagh, Co. Clare, Ireland, Nottingham University Expedition, viii.1961).

BIOLOGICAL NOTES. Six females were kept in the laboratory and all of them laid eggs erratically. Ten eggs were laid by one female and the oviposition period extended for thirty-one days. The eggs are relatively large in size and lustrous.

The outer surface of the chorion is densely covered with hair-like outgrowths. The eggs hatched in two to five days and the non-feeding larval stage lasted one to three days (average 2.44 days). The larva is sluggish. There are two feeding nymphal stages, the proto- and deutonymph. High mortality in the culture was observed for the protonymphs. The duration of the protonymphal stage was seven to twenty-two days (average 14.5 days). Two deutonymphs moulted into adult females and the duration of this stage was seven and twenty-one days, respectively. The nymphal and adult stages are very active and cannibalistic.

Pergamasus (Pergamasus) quisquiliarum (Can.)

Gamasus quisquiliarum Canestrini, G. & R. (1882). *Atti. Ist. Veneto*, **8** (5) : 920.
Gamasus (*Pergamasus*) *quisquiliarum* : Berlese, A. (1906). *Redia* **3** : 223, figs.
Pergamasus quisquiliarum : Cooreman, J. (1943). *Bull. Mus. roy. Hist. nat. Bel.* **19**, 63 : 7, fig. ; Halašková, V. (1959). *Zvlástni Otisk Mus. Zprávy Pražského Kraje* **4** : 3, figs. ; Schweizer, J. (1961). *Denks, schweiz. naturf. Ges.* **84** : 41, figs.

MALE. This species is deep yellow to reddish-brown in colour and well sclerotized. The dorsal shield (1,157–1,317μ long × 582–615μ wide) is without a transverse suture and is regionally reticulated. The opisthonotal shield is densely covered with setae, neotrichous (Text-fig. 61). Some dorsal setae appear to be pilose, under high magnification.

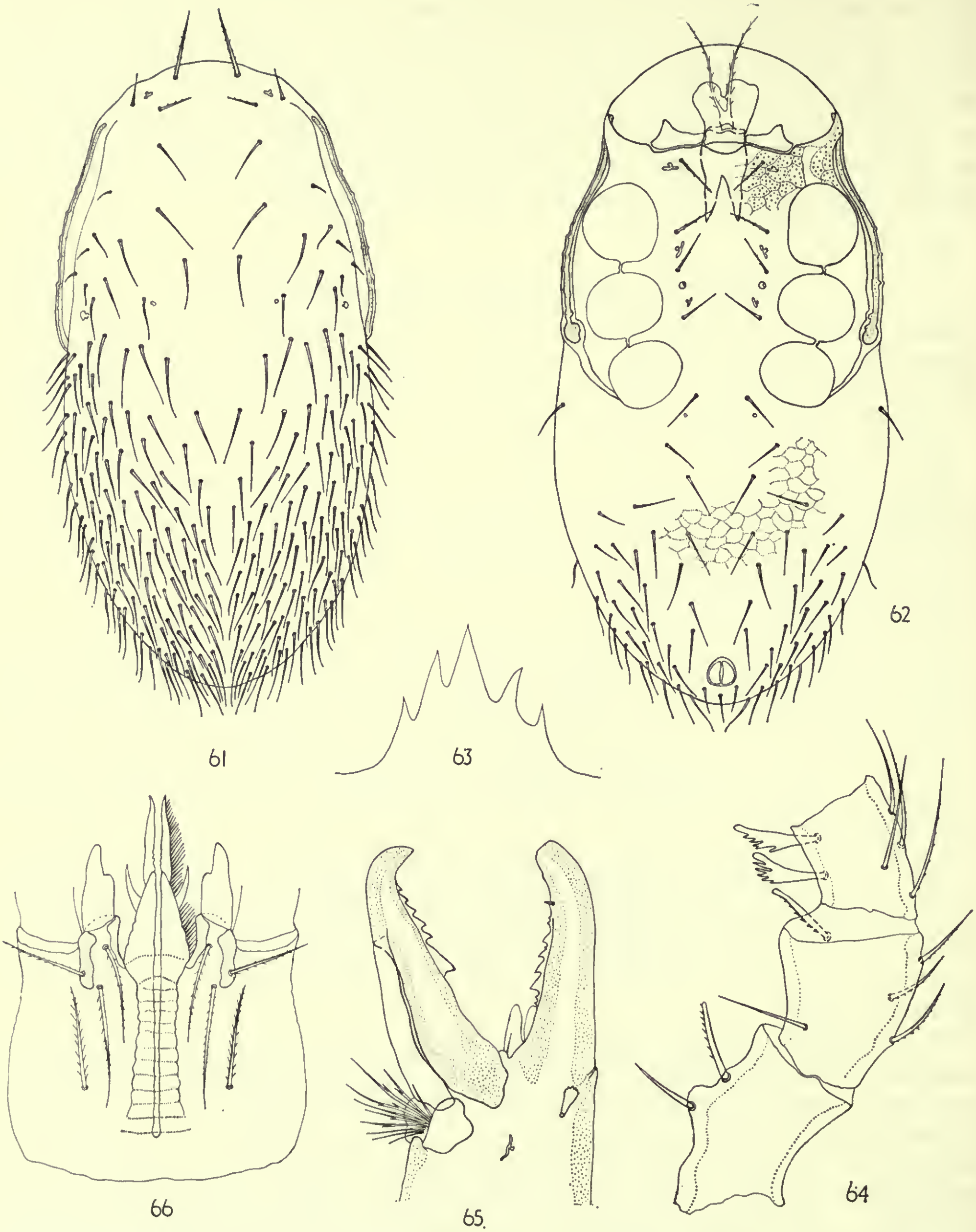
The tritosternum is well developed with a pair of pilose laciniae. The genital lamina has a median incision (Text-fig. 62). Two large prae-endopodal shields flank the genital sclerite. The pitted reticulation extends from the anterior margin of the sternal shield to a little behind coxae IV. The stigma is situated between coxae III and IV ; the peritreme anteriorly extends to coxa I and its outer margin is crenate. Posteriorly, the post-stigmatal prolongation of the peritrematal shield extends to coxa IV.

The tectum has five prongs (Text-fig. 63). The distinctive features of the pedipalp are shown in Text-fig. 64. The fixed digit of the chelicera is multi-dentate and the teeth are confined to the distal half of the digit. The fixed digit is truncated and the dorsal seta has a denticulated end (Text-fig. 65). The anterior lateral margins of the hypostomal processes are fringed (Text-fig. 66). The corniculus is stalked and is of distinctive shape.

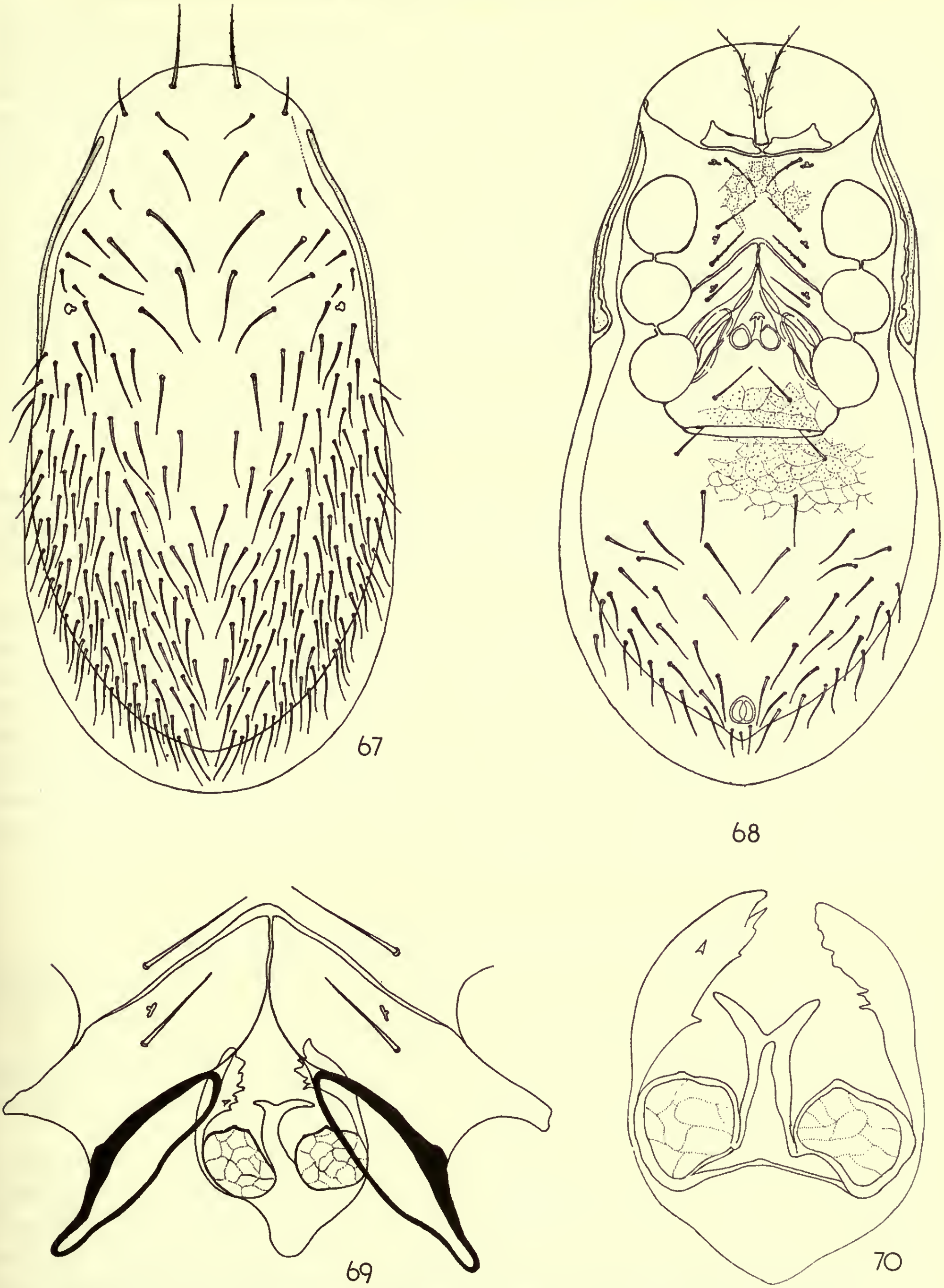
The tibia, tarsus and prae-tarsus of leg I are 254–312μ, 388–392μ and 45–49μ long, respectively. Leg II : the femur lacks an accessory spur and the main spur is distally truncated. The genual process is very weakly developed (Plates 1d & e). The tibia is provided with a vermiform process. The trochanter of leg IV is without any process.

FEMALE. The dorsal shield (1,317–1,417μ long × 764–815μ wide) is regionally reticulated. The podonotal shield is non-neotrichous, whilst the opisthonotal shield is densely covered with setae (Text-fig. 67).

The tritosternum has a pair of pilose laciniae. The tritosternal base is situated in a cup-like structure formed by a pair of prae-endopodal shields. The ventral shield



Figs. 61–66. *Pergamasus* (*Pergamasus*) *quisquiliarum* (Canestrini), male. Fig. 61 dorsum of idiosoma. Fig. 62 venter. Fig. 63 tectum. Fig. 64 trochanter, femur and genu of pedipalp. Fig. 65 chelicera. Fig. 66 venter of gnathosoma.



FIGS. 67–70. *Pergamasus* (*Pergamasus*) *quisquiliarum* (Canestrini), female. Fig. 67 dorsum of idiosoma. Fig. 68 venter. Fig. 69 genital region without epigynial shield. Fig. 70 bifurcated endogynial process.

is regionally ornamented with a pitted reticulation (Text-fig. 68). The metasternal shields are free and flank the epigynial shield. The genital shield is shown in Plate 7d. The endogynial process is complicated and its sacs are somewhat rounded in shape (Text-fig. 69). There is a median, elongated process in between the endogynial sacs, the terminal end of which may be bi- or trifurcated (Text-figs. 70 and 71). The stigma is situated between coxae III and IV ; the peritreme extends to coxa I. The entire peritrematal shield is fused with the dorsal shield.

The tectum and dentition of the chelicera are shown in Text-figs. 72 and 73 respectively. The pedipalp is essentially similar to that of the male (Text-fig. 74). Approximately half of the lateral margins of the hypostomal processes are fringed (Text-fig. 75). The deutosternal denticles are arranged in fourteen to sixteen transverse rows.

The tarsus (470–487µ long) of leg I is considerably longer than the tibia (350–367µ) ; the prae-tarsus is 29–55µ long. The trochanter of leg IV is without a tubercle.

Distribution and habitat. This species has previously been recorded from Italy (Canestrini & Canestrini, 1882), Norway (Berlese, 1906), Belgium (Cooreman, 1943), Czechoslovakia (Halašková, 1959), Switzerland (Schweizer, 1961) and South America (Sheals, 1962).

I have examined specimens from the following localities : Litter and soil under evergreen trees (St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 5.iv.1957). In leaf mould (Houghton Green, Rye, Sussex, J. T. Salmon, 19.v.1951). Bramble-covered ditch (Colletts Bridge, Norfolk, P. N. Lawrence). From soil (between Rockingham and Corby, Northants, B. N. K. Davies, 14.i.1958). Rotten reeds (Colletts Bridge, Norfolk, P. N. Lawrence). Litter under *Cupressus* sp. (Rothamsted Lodge, Rothamsted Experimental Station, Harpenden, Hertfordshire, G. Owen Evans and E. Browning, 18.iii.1957). Oak and beech litter (Singleton Park, Swansea, S. K. Bhattacharyya, 3.i.1961).

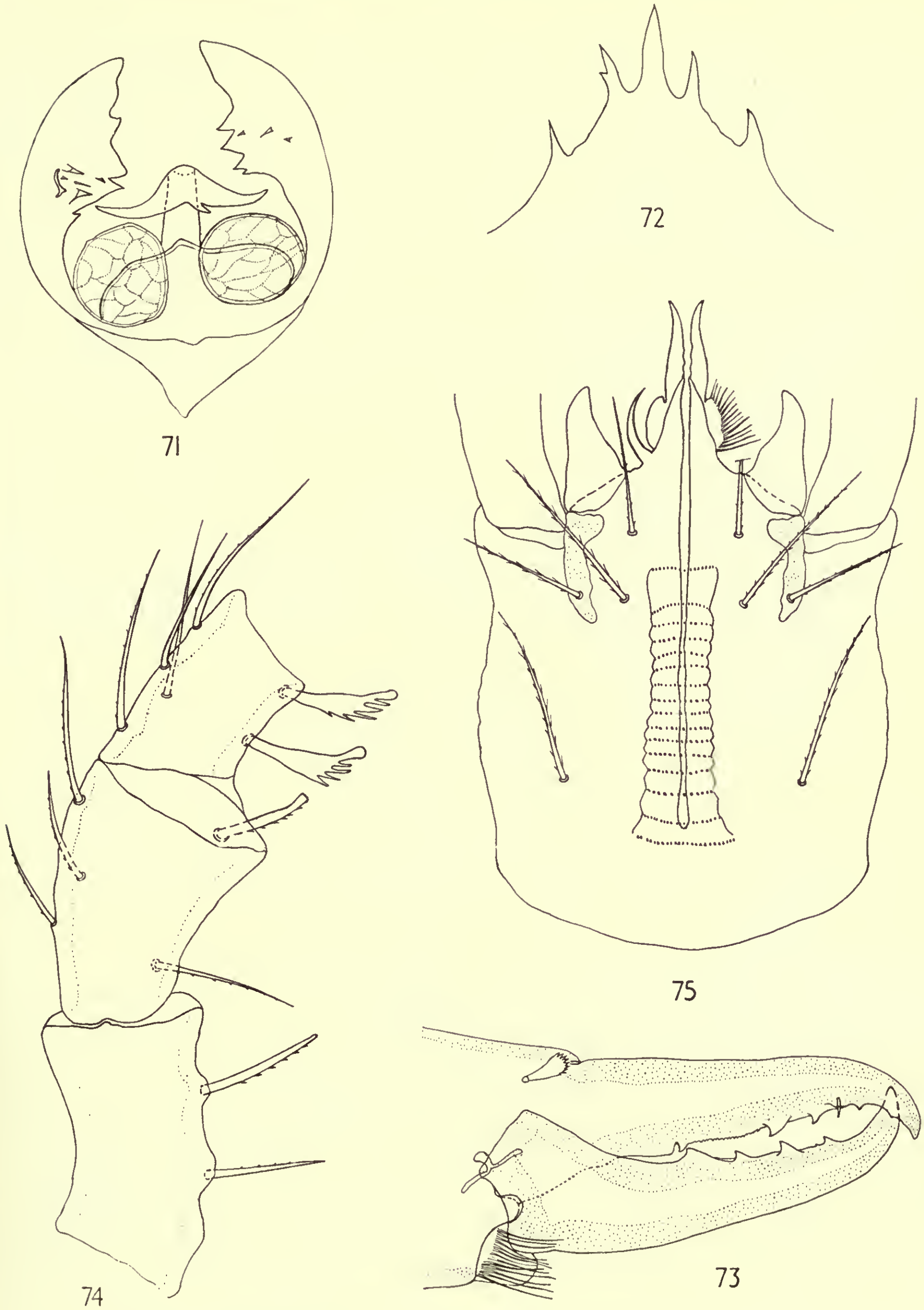
Pergamasus (Pergamasus) mirabilis Willmann

Pergamasus mirabilis Willmann, C. (1951). *SitzBer. Österr. Akad. Wiss.* Abt. 1, **160** : 99, figs.

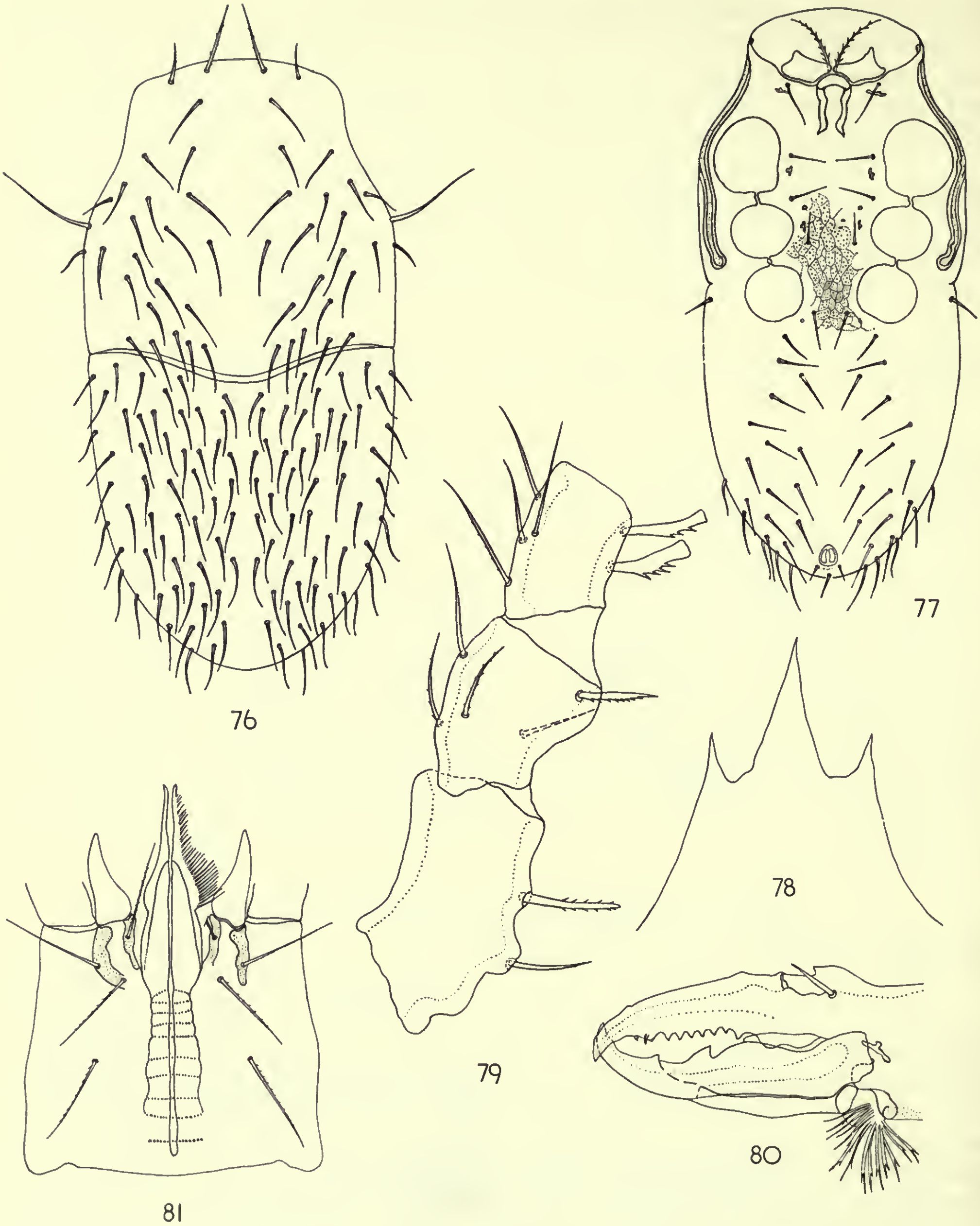
Amblygamasus mirabilis : Schweizer, J. (1961). *Denks. schweiz. naturf. Ges.* **84** : 66, figs.

Male. The dorsal shield (771–838µ long × 400–424µ wide) is reddish in colour and has a transverse suture (Text-fig. 76). Some dorsal setae appear to be pilose under high magnification.

The form of the prae-endopodal shields is shown in Text-fig. 77. The tritosternum has a pair of pilose laciniae but the tritosternal base is completely hidden by the genital lamina. The setation of the opisthogastral shield is figured. The pitted reticulation extends from the anterior margin of the sternal shield to a little behind the coxa of leg IV. The stigma is situated between coxae III and IV ; and the undulating peritreme reaches to coxa I. A pair of post-stigmatal setae is present.



FIGS. 71–75. *Pergamasus* (*Pergamasus*) *quisquiliarum* (Canestrini), female. Fig. 71 trifurcated endogynial process. Fig. 72 tectum. Fig. 73 chelicera. Fig. 74 trochanter, femur and genu of pedipalp. Fig. 75 venter of gnathosoma.



FIGS. 76–81. *Pergamasus* (*Pergamasus*) *mirabilis* Willmann, male. Fig. 76 dorsum of idiosoma. Fig. 77 venter. Fig. 78 tectum. Fig. 79 trochanter, femur and genu of pedipalp. Fig. 80 chelicera. Fig. 81 venter of gnathosoma.

The tectum is three-pronged, the median being longer and broader than the lateral tines (Text-fig. 78). The palpal trochanter, femur and genu are shown in Text-fig. 79. The chelicera is rather elongated with well developed dentition, (Text-fig. 80). A cone-shaped projection is especially discernible above the dorsal seta of the chelicera. The fixed digit is not truncated and has a simple dorsal seta. The teeth of the movable digit are well separated and the spermadactyl is normal. The corniculus is stalked ; and more than the distal half of the hypostomal processes is provided with fringes. The deutosternal denticles in the ventral groove of the gnathosoma are shown in Text-fig. 81.

The tibia (162–168μ) of leg I is remarkably shorter than the tarsus (221–247μ) ; the prae-tarsus is only 17–25μ long. The coxa of leg II has well-developed spurs (Plate 2a). The femur of leg II is not crassate (Plate 2b). The genu has a large falcate spur, and the tibia is devoid of processes. The trochanter of leg IV possesses no spur.

FEMALE. Unknown.

DISTRIBUTION AND HABITAT. This species is previously recorded from Austria (Willmann, 1951) and Switzerland (Schweizer, 1961).

I have examined specimens from soil (between Rockingham and Corby, Northants, B. N. K. Davis, 14.i.1958).

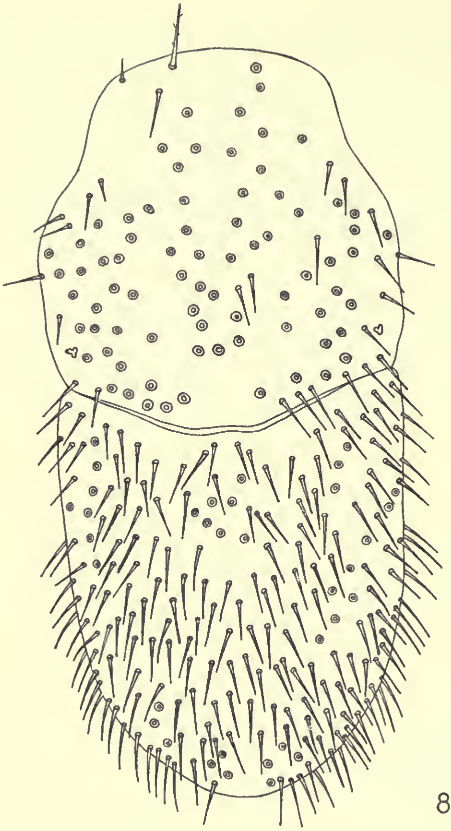
Pergamasus (Pergamasus) hamatus (C. L. Koch) Berlese, 1906

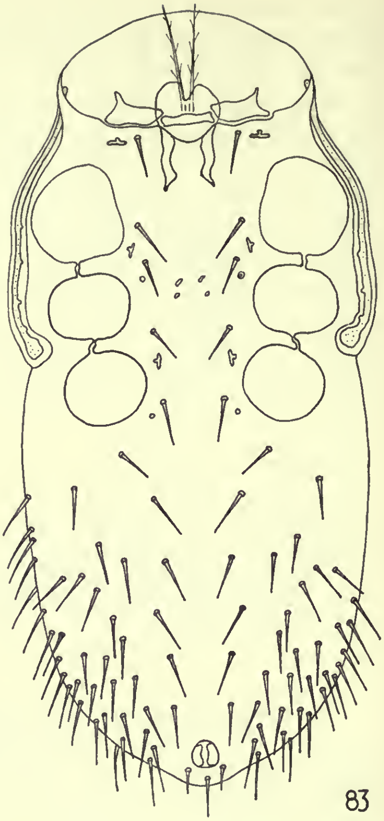
Gamasus hamatus Koch, C. L. (1839). *Deutsch. Crust. Myr. Arachn.* fasc. 26 t. 2.
Gamasus (*Pergamasus*) *hamatus* : Berlese, A. (1906). *Redia* **3** : 212, figs.
Gamasus (*Pergamasus*) *hamatus* var. *gracilis* Berl. (sic) : Berlese, A. (1906). *Redia* **3** : tab. V, fig. Tab. XIV, figs.
Pergamasus hamatus : Schweizer, J. (1961). *Denks. schweiz. naturf. Ges.* **84** : 61, figs.
Pergamasus hamatus (Koch) var. *longipes* Schweizer, J. (1961). *Denks. schweiz. naturf. Ges.* **84** : 62, figs.

MALE. The dorsal shield (1,157μ long × 582μ wide) is strongly sclerotized and provided with a median transverse suture. This species differs from other neotrichous species in that the neotrichy extends into the podonotal region of the dorsal shield (Text-fig. 82). Some dorsal setae appear pilose under high magnification.

Ventrally, the tritosternum has a pair of well-developed pilose laciniae but the tritosternal base is completely hidden by the genital lamina. The distribution of the prae-endopodal shields, and the shape of the genital lamina, is shown in Text-fig. 83. The setation of the opisthogastral shield is figured. The stigma is situated between coxae III and IV ; the peritreme extends to coxa I. The peritrematal shield lies along the dorso-ventral margin of the body.

The tectum is three-pronged, the median prong being longer than the lateral ones (Text-fig. 84). The dorsal surface of the tectum is faintly reticulated. The pedipalp trochanter is tuberculated (Text-fig. 85) ; the femur and genu are provided with one comb-like and two palmate setae, respectively. The fixed digit of the chelicera has



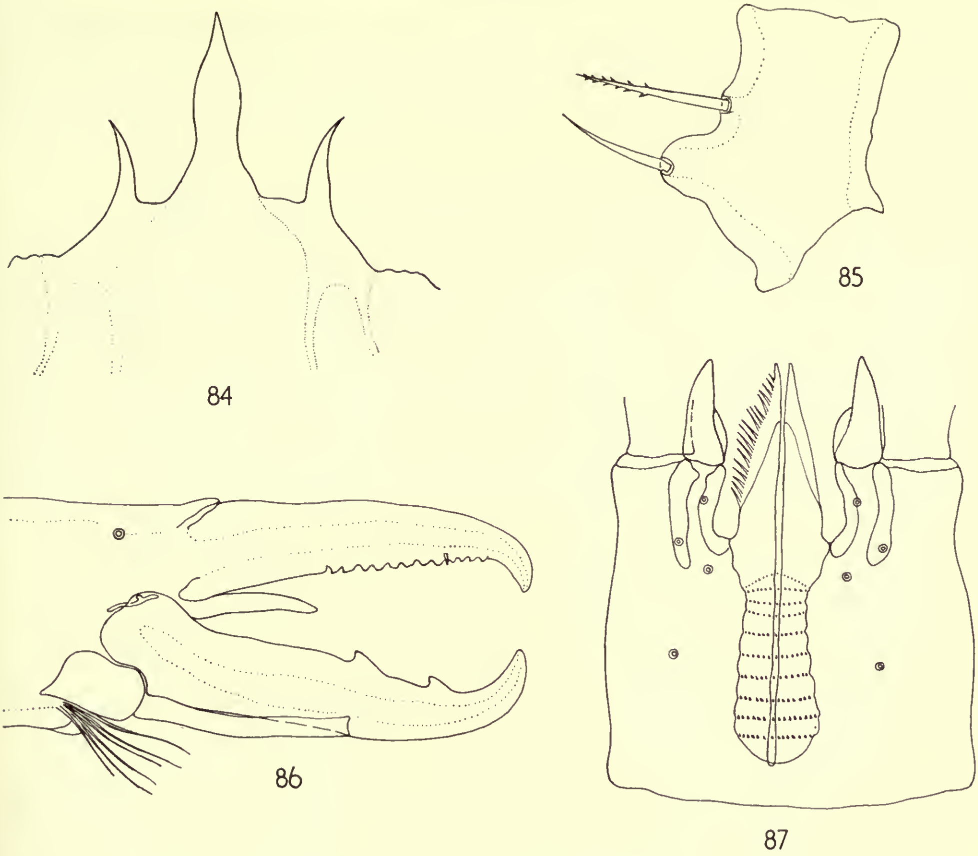


FIGS. 82–83. *Pergamasus* (*Pergamasus*) *hamatus* (Koch), male.
Fig. 82 dorsum of idiosoma. Fig. 83 venter.

a row of closely-set teeth ; the movable digit is bidentate with a normal spermadactyl (Text-fig. 86). The terminal ends of both digits are pointed and the arthrodial membranes are simple and branched. The corniculus has a distinct stalk and its peculiar shape is shown in Text-fig. 87. The fringed hypostomal processes are as figured. The deutosternal denticles on the ventral groove of the gnathosoma are arranged in ten transverse rows.

The tibia, tarsus and prae-tarsus of leg I are 254μ, 333–337μ and 41μ long respectively. The distinctive feature of leg II is shown in Plate 2c. The femur has a relatively small main falcate spur at the base of which is an elongated accessory spur. The genu and tibia are armed with conical rather than elongate spurs. The trochanter of leg IV is without any prominence.

FEMALE. The dorsal shield (1,200–1,268μ long × 665μ wide) tapers posteriorly. The setation of the dorsal shield is similar to that of the male (Text-fig. 88).

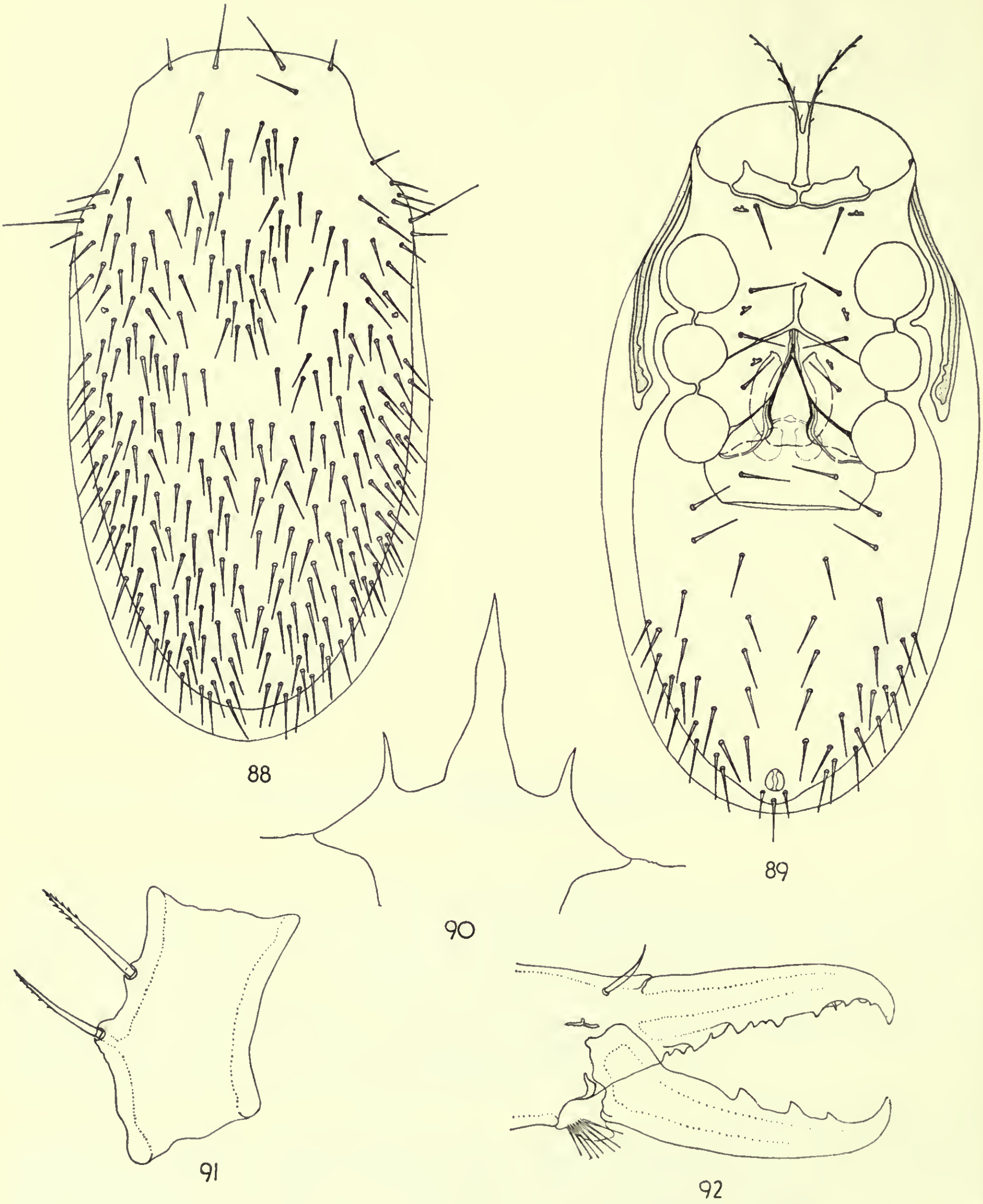


FIGS. 84–87. *Pergamasus* (*Pergamasus*) *hamatus* (Koch), male.
Fig. 84 tectum. Fig. 85 trochanter of pedipalp. Fig. 86 chelicera. Fig. 87 venter of gnathosoma.

The tritosternum is well developed with an elongated basal part and a pair of pilose laciniae. A pair of large prae-endopodal shields is present. The sternal shield is furnished with a median vertical groove which anteriorly reaches to about the level of sternal setae II. The metasternal shields may be fused. The endogynium has a pair of horns. The endogynial processes are relatively simple. The setation of the opisthogastral shield is shown in Text-fig. 89. The stigma is situated between coxae III and IV ; the peritreme extends to coxa I. The antero-lateral margin of the peritrematal shield is coalesced with the dorsal shield at the level of coxa II, but the shield is free posteriorly.

The tectum is three-pronged (Text-fig. 90). The pedipalp is essentially similar to that in the male (except the trochanter, which lacks a tubercle, Text-fig. 91). The fixed digit is furnished with a row of closely-set teeth : the movable finger is tridentate, the teeth being well separated (Text-fig. 92).

Leg I with the tibia, tarsus and prae-tarsus 270μ, 350–367μ and 37μ long, respectively.



FIGS. 88–92. *Pergamasus* (*Pergamasus*) *hamatus* (Koch), female. Fig. 88 dorsum of idiosoma. Fig. 89 venter. Fig. 90 tectum. Fig. 91 trochanter of pedipalp. Fig. 92 chelicera.

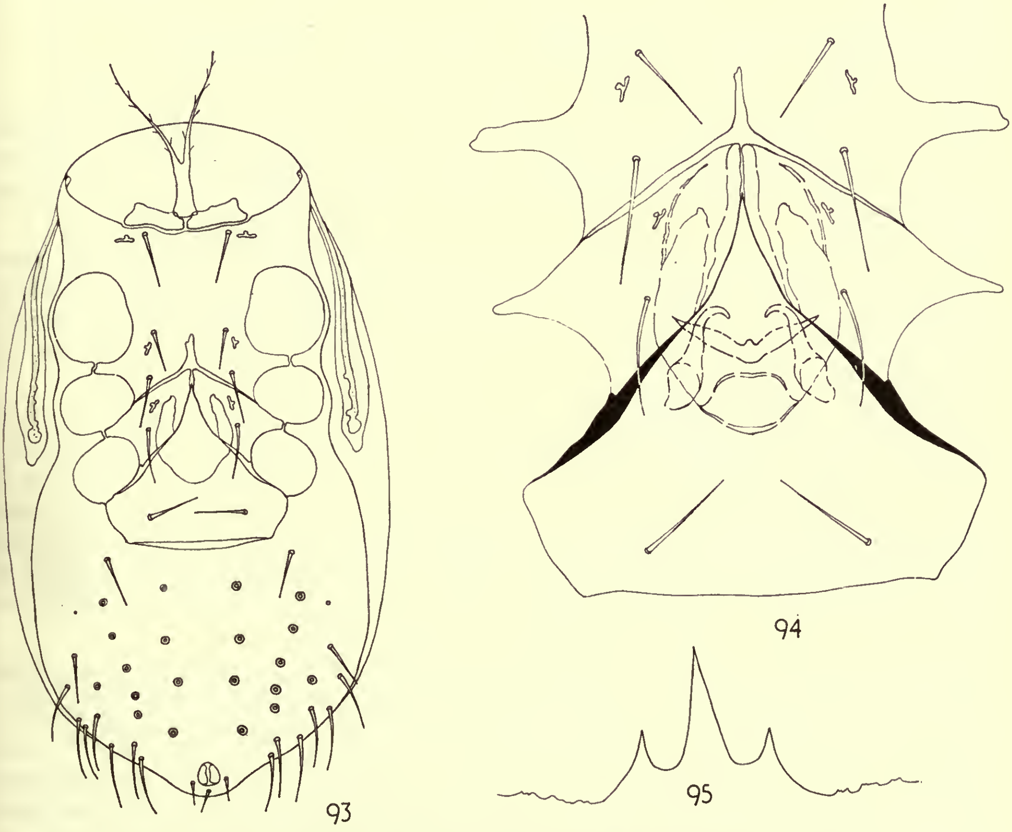
Distribution and habitat. This species has been recorded from Germany (Koch, 1839), Italy (Berlese, 1906) and Switzerland (Schweizer, 1961).

I have examined specimens from Brigster, Lancashire, and bulk soil, Ayside, Westmorland (J. Satchell, xi.1953).

Pergamasus (Paragamasus) hortensis sp. nov.

Female. The dorsal shield, in the compressed specimen, measures about 1,200μ long and 683μ wide, and is lightly sclerotized and yellow in colour. The chaetotaxy of the opisthonotal region shows neotrichy (Text-fig. 93).

Ventrally, the tritosternum has an elongate basal part and a pair of pilose laciniae. A pair of large prae-endopodal shields is present. The posterior margin of the sternal shield is provided with a short, median vertical fissure. The metasternal shields are free. The endogynial horns and processes are delineated in Text-fig. 94. The setation of the opisthogastral shield is figured. The stigma is situated between



Figs. 93–95. *Pergamasus* (*Pergamasus*) *hortensis* sp. nov., female.
Fig. 93 venter. Fig. 94 magnified structure of the sterniti-genital region. Fig. 95 tectum.

coxae III and IV ; the peritreme extends to coxa I. The peritrematal shield is free posteriorly.

The tectum has three prongs (Text-fig. 95). The chelicerae of the unique specimen have not been examined. The most distinctive features of the pedipalp are, the femur with a comb-like seta and the genu with two spatulate setae. The hypostomal process is similar to that in *P.* (*P.*) *quisquiliarum.*

Leg I with tibia, tarsus and prae-tarsus 274–279μ, 354μ and 43–45μ long respectively. The trochanter of leg IV is without any tubercle.

MALE. Unknown.

HABITAT. I have examined a single damaged female from greenhouse soil, Marton, Blackpool, Lancashire, M. Cohen, 1934 (Holotype 1963.2.7.10).

Pergamasus (Paragamasus) robustus (Oudemans)

Parasitus longulus (C. L. Koch), var. *robustus* Oudemans, A. C. (1902). *Tijdschr. Ent.* **45** : 38, figs.
Parasitus robustus : Oudemans, A. C. (1905). *Abh. Nat. Ver. Bremen* **18** : 82.
Gamasus (*Pergamasus*) *robustus :* Berlese, A. (1906). *Redia* **3** : 219, figs.
Pergamasus robustus : Trägårdh, I. (1910). *Naturw. Untersuch. Sarekgeb.* **4** (4) : 404, figs.

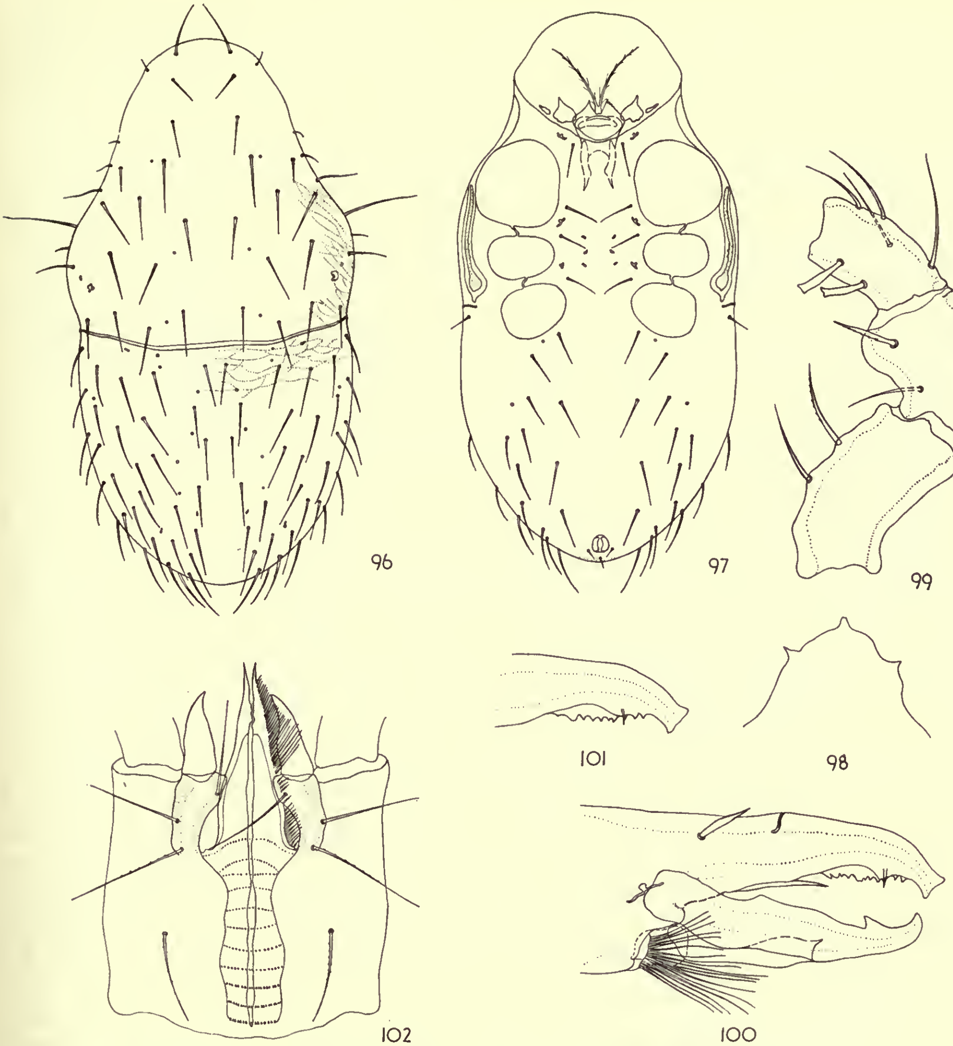
MALE. The dorsal shield (1,100–1,200μ long × 615–665μ wide) has a median transverse suture (Text-fig. 96). The podonotal region bears twenty-one pairs of setae and their distribution is figured. The opisthonotal region has a variable number of setae.

The tritosternum has a pair of well-developed ciliated laciniae. The genital lamina is distinctive in shape (Text-fig. 97). The anterior margin of the sternal shield is slightly concave. The setation of the opisthosomal region is figured. The stigma is situated between coxae III and IV ; the peritreme extends to coxa II. A pair of post-stigmatal setae is present.

The tectum is rounded in shape and provided with three prongs (Text-fig. 98). The most distinctive features of the chaetotaxy of the pedipalp are, the comb-like seta on the femur and the two spatulate setae on the genu. The palpal trochanter is without any tubercle (Text-fig. 99). The chelicera is robust, the fixed digit being truncated and with a variable number of teeth (Text-figs. 100 & 101). The movable digit is unidentate with a normal spermadactyl. There are ten transverse rows of deutosternal denticles. The entire outer margins of the hypostomal processes are fringed (Text-fig. 102). The corniculus is distinctly stalked.

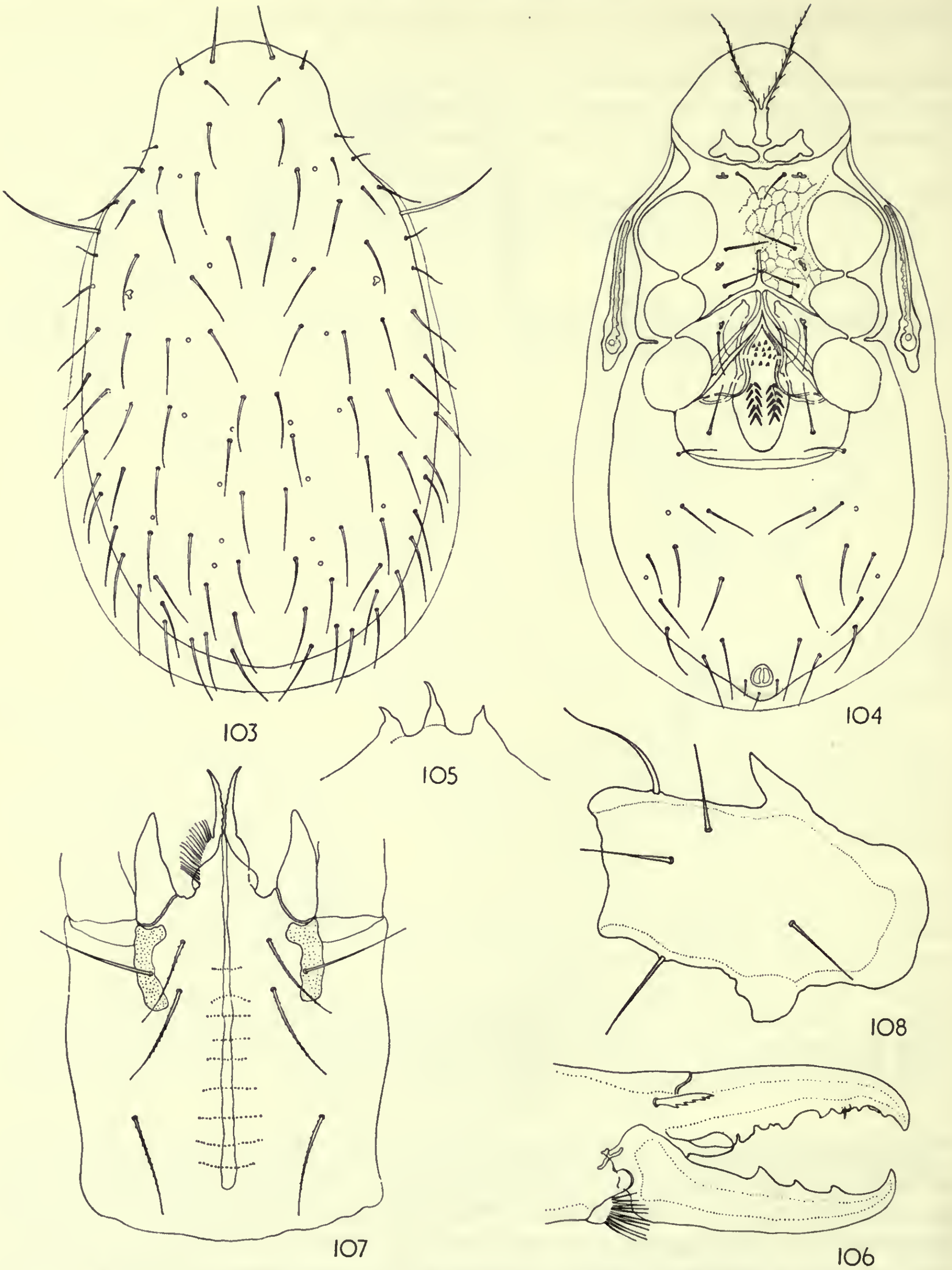
The tibia, tarsus and prae-tarsus of leg I are 183–188μ, 237–258μ and 17–25μ long respectively. The distinctive features of leg II are shown in Plate 2d and Plate 3f ; the trochanter being spurred. The trochanter of leg IV is devoid of processes.

FEMALE. The dorsal shield (1,117μ long × 598–632μ wide) is regionally reticulated. The anterior half of the dorsal shield is furnished with twenty-one pairs of setae, whilst the number of setae on the posterior half is greatly variable (Text-fig. 103).



FIGS. 96–102. *Pergamasus* (*Paragamasus*) *robustus* (Oudemans), male. Fig. 96 dorsum of idiosoma. Fig. 97 venter. Fig. 98 tectum. Fig. 99 trochanter, femur and genu of pedipalp. Fig. 100 chelicera. Fig. 101 variation in the dentition of the fixed digit. Fig. 102 venter of gnathosoma.

The tritosternum has a well-developed basal part. There is a granulated region in between a pair of large prae-endopodal shields. The sternal shield bears three pairs of setae and two pairs of pores. Posteriorly the sternal shield has a median narrow incision reaching the level of sternal setae II. The metasternal shields are free. A pair of endogynial horns is present. The endogynial processes are very complicated (Text-fig. 104). The genital shield is shown in Plate 7e. The stigma is situated between coxae III and IV ; the extension of the peritreme is as in the male.



FIGS. 103–108. *Pergamasus* (*Paragamasus*) *robustus* (Oudemans), female.
Fig. 103 dorsum of idiosoma. Fig. 104 venter. Fig. 105 tectum. Fig. 106 chelicera.
Fig. 107 venter of gnathosoma. Fig. 108 trochanter of leg IV.

The tectum is three-pronged (Text-fig. 105). The pedipalp is essentially similar to that of the male. The dorsal seta of the fixed digit is pilose ; the movable digit of the chelicera is tridentate (Text-fig. 106). The structure of the gnathosoma is shown in Text-fig. 107.

The tibia, tarsus and prae-tarsus of leg I are 183–187μ, 254–258μ and 17–21μ long respectively. The trochanter of leg IV may be with or without any processes (Text-fig. 108).

DISTRIBUTION AND HABITAT. This species has been recorded from Holland (Oudemans, 1902), Germany, Norway (Berlese, 1906), and Swedish Lapland (Trägårdh, 1910).

I have examined the following material : Litter and humus under pines and holly (near Duddleswell, Ashdown Forest, Sussex, K. H. Hyatt, 10.ix.1956). Moss and leaves (Adelaide Hill, Bowness, Cumberland, J. T. Salmon, 29.vi.1951). *Sphagnum*, etc. (Cock Hill, Yorkshire, J. T. Salmon, 21.vii.1951). In leaf mould (Epping Forest, Essex, J. T. Salmon, 27.v.1951). In leaf mould (Savernake Forest, Berkshire, J. T. Salmon, 26.ix.1951). In leaf mould (Forest of Dean, Gloucestershire, J. T. Salmon, 27.ix.1951), (Stratton Strawless, near Aylsham, Norwich, Norfolk, J. T. Salmon, 13.v.1951). In moss (Grassington, Grass Woods, North Riding, Yorkshire, J. T. Salmon, 24.vi.1951). *Sphagnum* (Ascot, Berkshire, A. H. G. Alston, 8.xii.1957). Moss on tree stumps and stones (Forest of Dean, Gloucestershire, J. T. Salmon, 27.ix.1951), (Red Bank, Grasmere, Westmorland, M. E. Bacchus, 3.xii.1954). In oak and beech leaf mould (Grasmere, Westmorland, J. T. Salmon, 26.vi.1951). In leaf mould (Boltons Wood, Boltons Abbey, North Riding, Yorks., J. T. Salmon, 24.vi.1951). In leaf mould (Burnham Beeches, Buckinghamshire, J. T. Salmon, 3.v.1951). *Sphagnum*, etc. (Moel Siabod, North Wales, P. N. Lawrence, 22.x.1960). Rotten stump (Gwydyr Forest, North Wales, P. N. Lawrence, 22.x.1960). Oak humus (Gwydyr Forest, North Wales, P. N. Lawrence, 22.x.1960). In moss (Tarbert, Crianlarich, Loch Lomond, Dunbarton, J. T. Salmon, 3.vii.1951). Floor of scotch fir wood (Aviemore, Inverness, J. T. Salmon, 7.vii.1951). In moss and heather (Glen Garry, Perth, Meall Doire and Daimh, J. T. Salmon, 5.vii.1951).

BIOLOGICAL NOTES. Two females collected from oak litter were reared under laboratory conditions. Twenty eggs were laid by one female and twenty-two eggs by the other. The female which laid twenty eggs lived for eighty-eight days in culture. The eggs are smooth and considerably smaller in size than those of *P.* (*P.*) *crassipes* or *P.* (*P.*) *septentrionalis*. The eggs hatched in three to five days (average 4·5 days) after deposition and the active feeding larval stage lasted five to seventeen days (average 9·08 days). The duration of the protonymphal and deutonymphal stages was seven to fifteen (average 10·18 days) and fourteen to twenty-three (average 20·0) days, respectively. Both these instars were active and fed voraciously on Collembola. Cannibalism was also noted.

The eight deutonymphs reared all moulted to give males. These males resembled the parent female in lacking a tubercle on the trochanter of leg IV. There were no tubercles on the trochanters of the pedipalps in the reared males.

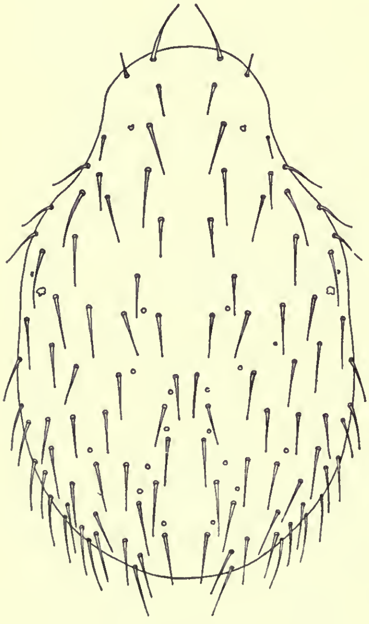
Pergamasus (Paragamasus) alpestris Berlese

Gamasus (*Pergamasus*) *alpestris* Berlese, A. (1904). *Redia* **1** : 236 ; Berlese, A. (1906). *Redia* **3** : 220, figs.

Pergamasus alpestris : Cooreman, J. (1954). *Bull. Inst. roy. Sci. nat. Belg.* **30,** 34 : 5, figs. Halašková, V. (1959) *Zvláštni Otisk Mus. Zprávy Pražského Kraje* **4** : 3, figs. ; Schweizer, J. (1961) *Denks. schweiz. naturf. Ges.* **84** : 63, figs.

MALE. The dorsum is dark brown in colour and sub-globular in shape. The dorsal shield (1,150–1,190μ long × 632–648μ wide) has no transverse suture and the lengths of the dorsal setae are variable (Text-fig. 109).

The prae-endopodal shields and the shape of the genital lamina are shown in Text-fig. 110. The tritosternum has an extremely reduced base and a pair of pilose laciniae.



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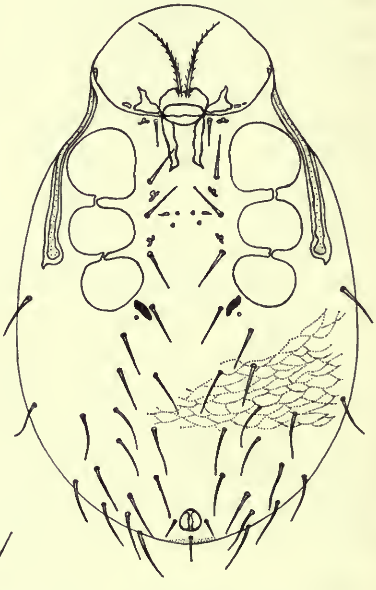

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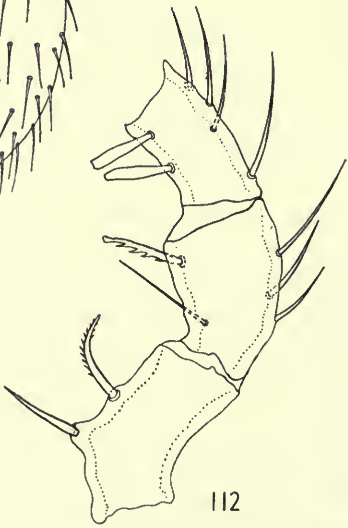

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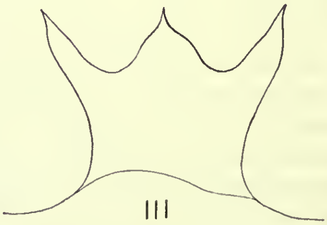

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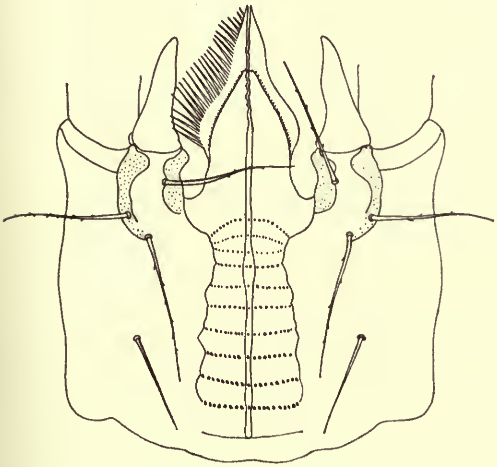
FIGS. 109–112. *Pergamasus* (*Paragamasus*) *alpestris* Berlese, male.
Fig. 109 dorsum of idiosoma. Fig. 110 venter. Fig. 111 tectum. Fig. 112 trochanter, femur and genu of pedipalp.

The venter is very characteristic ; a scaly, elongated structure is situated near the coxa of leg IV. The setation of the opisthogastral shield is figured. The stigma is situated between the coxae III and IV ; and the peritreme extends to coxa I. A pair of relatively long post-stigmatal setae is present.

The tectum is three-pronged and situated on a cup-like structure (Text-fig. 111). The distinctive features of the pedipalp and chelicerae are shown in Text-figs. 112 and 113 respectively. The corniculus is distinctly stalked ; and the hypostomal process fringed (Text-fig. 114). The deutosternal denticles are arranged in ten transverse rows.

The tibia, tarsus and prae-tarsus of leg I are 204–208μ, 300–304μ and 21–25μ long respectively. Leg II, with coxa, trochanter, femur, genu and tibia, is armed with variously shaped spurs (Plate 2f). Leg II is remarkable for the presence of a spur on the coxa (Plate 2e). The femur is crassate with a well-developed falcate major spur and accessory spurs. The armature of the trochanter of leg IV is shown in Text-fig. 115.

Female. The dorsal shield (1,117–1,132μ long × 732μ wide) is broadly oval and regionally reticulated (Text-fig. 116). Lengths of the dorsal setae are greatly variable. The posterior half of the shield bears about twenty-nine pairs.



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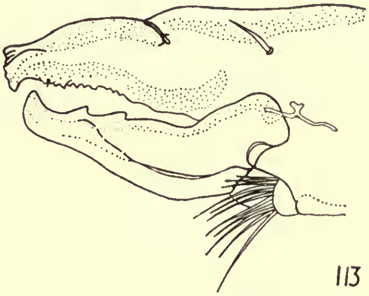

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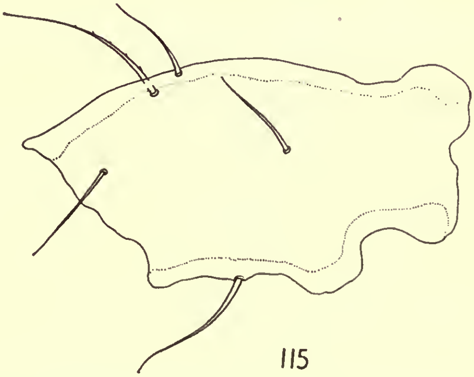

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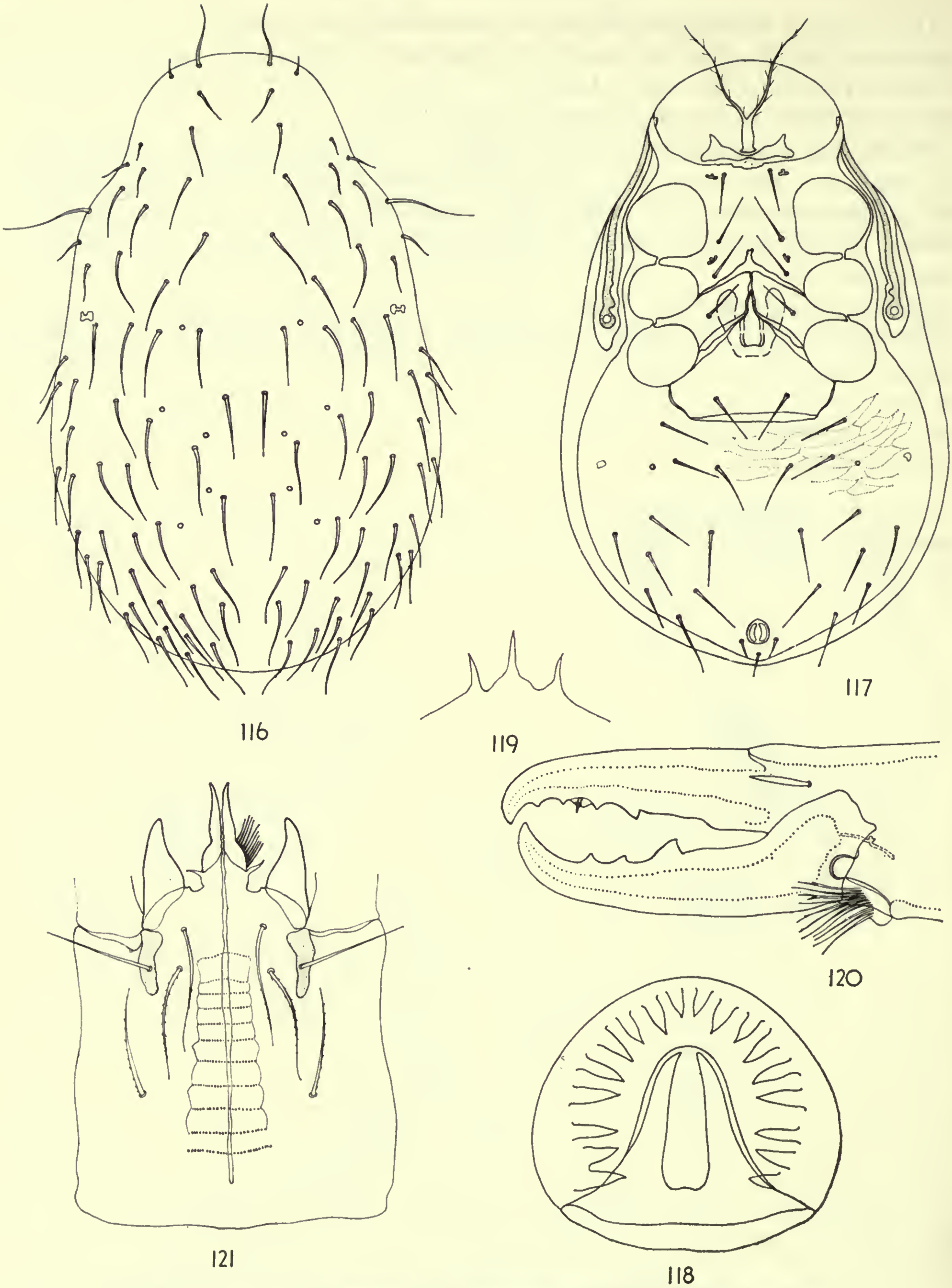
Figs. 113–115. *Pergamasus* (*Paragamasus*) *alpestris* Berlese, male.
Fig. 113 chelicera. Fig. 114 venter of gnathosoma. Fig. 115 trochanter of leg IV.



Figs. 116–121. *Pergamasus* (*Paragamasus*) *alpestris* Berlese, female. Fig. 116 dorsum of idiosoma. Fig. 117 venter. Fig. 118 endogynial process. Fig. 119 tectum. Fig. 120 chelicera. Fig. 121 venter of gnathosoma.

Ventrally, the tritosternum has an elongated basal part and a pair of well-developed pilose laciniae. There is a pair of large prae-endopodal shields which are coalesced in the median line. The metasternal shields are free (Text-fig. 117). The endogynium has a pair of horns. The endogynial process is complicated (Text-fig. 118). The genital shield is as seen in Plate 7f. The opisthogastral shield is furnished with ten pairs of setae (excepting paranal and post-anal setae) of variable length. The stigma is in the normal position with the anterior prolongation of the peritreme to coxa I.

The tectum is three-pointed (Text-fig. 119). The chelicera is shown in Text-fig. 120. The proximal half of the hypostomal margins are fringed. The deutosternal denticles are arranged in parallel transverse rows (Text-fig. 121).

The tarsus (287–289μ) of leg I is considerably longer than the tibia (187–196μ). The prae-tarsus (29–30μ) is long.

DISTRIBUTION AND HABITAT. This species is previously known from Italy (Berlese, 1904, 1906), Belgium (Cooreman, 1954), Czechoslovakia (Halašková, 1959), Switzerland (Schweizer, 1961).

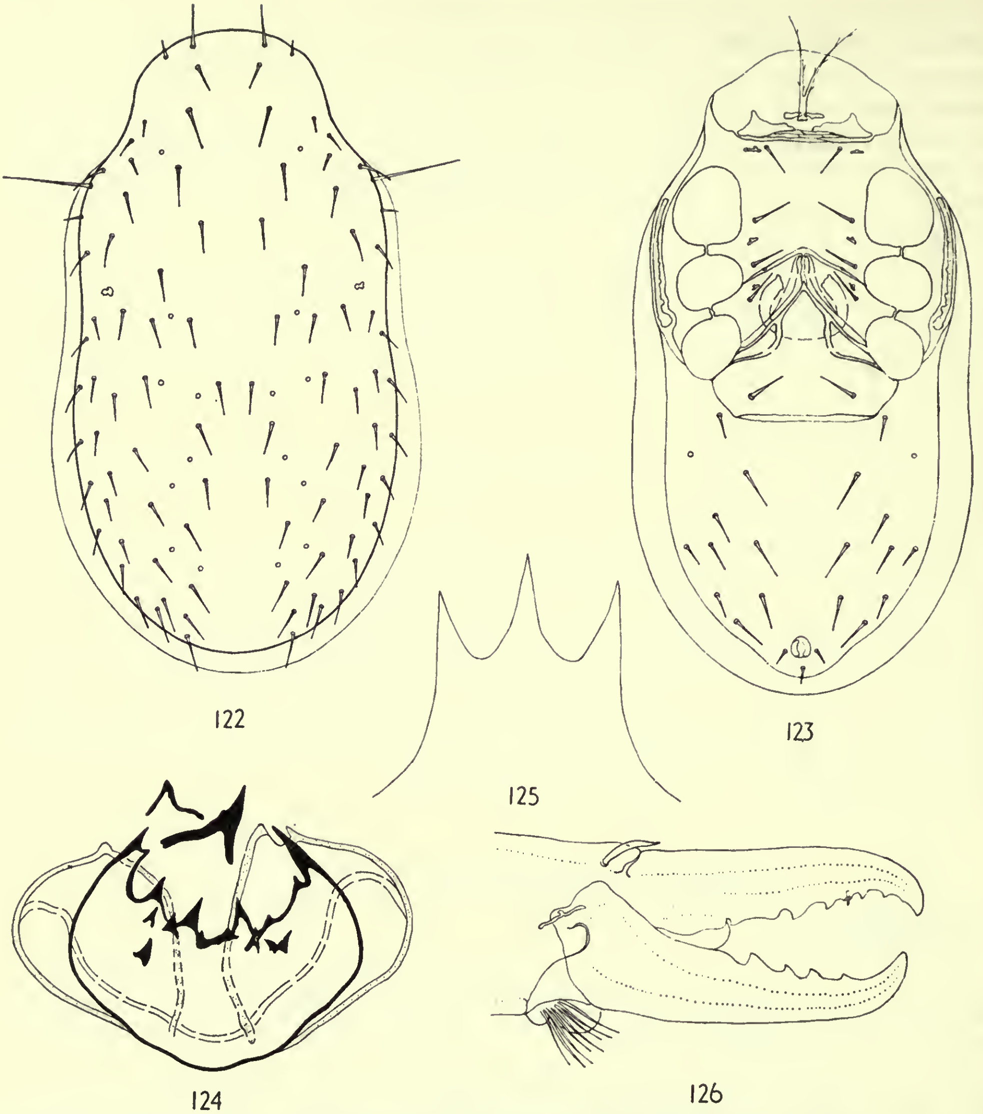
I have examined material from moss on tree stumps and stones (Forest of Dean, Gloucestershire, J. T. Salmon, 27.ix.1951 ; Red Bank, Grasmere, Westmorland, M. E. Bacchus, 3.xii.1954) ; peat (Blackbush, Kew, Surrey, A. H. G. Alston, 18.i.1958) ; moss from crevices in rocks (near Force Forge, Westmorland, M. E. Bacchus, 2.xii.1954) ; leaf mould (Boltons Wood, Boltons Abbey, North Riding, Yorks., J. T. Salmon, 24.vi.1951) ; in moss of wall (Tarn Howes, North Lancashire, M. E. Bacchus, 4.xii.1954) and yew and rhododendron humus (Educational Garden, Swansea University, P. N. Lawrence, 26.iii.1962).

Pergamasus (Paragamasus) alstoni sp. nov.

MALE. Unknown.

FEMALE. The dorsal shield (622–648μ long × 350–357μ wide) is sclerotized, regionally reticulated and yellow in colour. The setation of the dorsal shield is shown in Text-fig. 122.

The tritosternum has a pair of pilose laciniae. The distribution of the prae-endopodal shields is characteristic (Text-fig. 123). The interscutal membrane between the anterior margin of the sternal shield and the large prae-endopodal shields is striated. The metasternal shields are free. The endogynium has a pair of horns and its process is remarkable in shape and structure (Text-fig. 124). The genital shield is shown in Plate 7g. The opisthogastral shield has nine pairs of setae (excepting three setae associated with the anus). The stigma is situated between coxae III and IV ; and the peritreme extends as far as the level of coxa II. The peritrematal shield is characteristically fused with the exopodal and opisthogastral shields. The posterior extremity of the peritrematal shield curves inwards in a tubular form to meet coxa IV.



FIGS. 122–126. *Pergamasus* (*Paragamasus*) *alstoni* sp. nov., female.
Fig. 122 dorsum of idiosoma. Fig. 123 venter. Fig 124. endogynial process. Fig. 125 tectum. Fig. 126 chelicera.

The tectum is three-pronged (Text-fig. 125). The distinctive features of the pedipalp are : femur with a comb-like seta and genu with two spatulate setae. The dentition and shape of the chelicera are shown in Text-fig. 126. The ventral groove of the gnathosoma possesses ten or eleven rows of deutosternal denticles.

The tibia, tarsus and prae-tarsus of leg I are 95–102μ, 150–154μ and 12–17μ long respectively. The trochanter of leg IV is devoid of a tubercle.

HABITAT. I have examined three females from soil in filmy-fern house (Royal Physic Garden, Chelsea, London, A. H. G. Alston, January, 1956) and a single female from yew and rhododendron humus (Educational Garden, Swansea University, Swansea, P. N. Lawrence, 26.iii.1962).

I have designated a female from the Royal Physic Garden, Chelsea, London (Coll. A. H. G. Alston, January, 1956) as the Holotype (1963.2.7.16).

Pergamasus (Paragamasus) armatus Halbert

Gamasus (*Pergamasus*) *runciger* Berl. var. *armatus* Halbert, J. N. (1915). *Proc. R. Irish Acad.* **31** 39 ii : 51, figs.

MALE. The dorsal shield (838–898μ long × 433μ wide) is provided with a median transverse suture. The anterior dorsal shield is furnished with twenty-one pairs of setae and the setation of the posterior half is shown in Text-fig. 127.

The placement of the prae-endopodal shields and the shape of the genital lamina is shown in Text-fig. 128. The tritosternum has a reduced basal part and a pair of ciliated laciniae. The setation of the opisthogastral shield is shown in the figure. The stigma is situated between coxae III and IV ; the peritreme extends to coxa I. A pair of post-stigmatal setae is present.

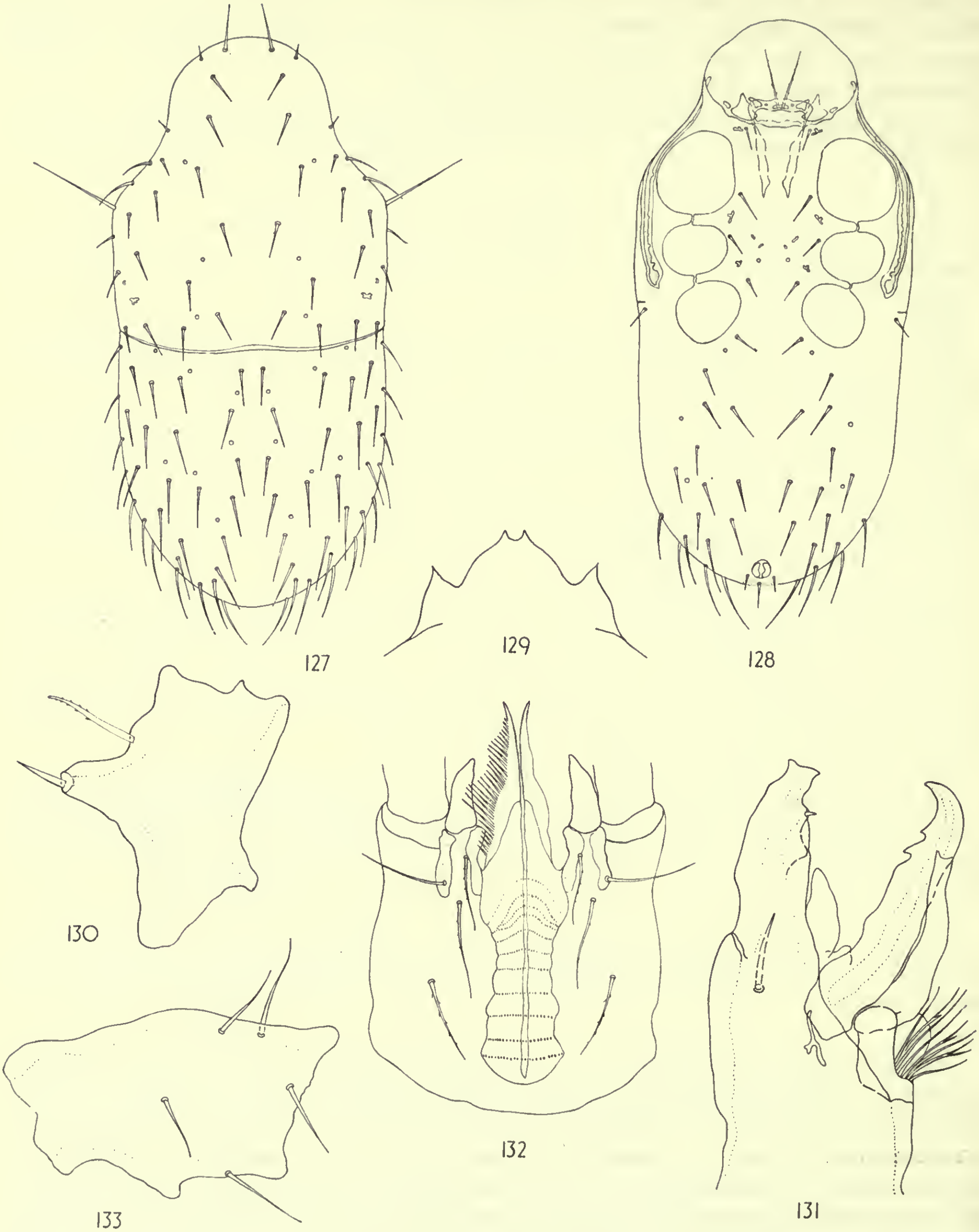
The tectum is shown in Text-fig. 129. The palpal trochanter has a large seta-bearing protuberance (Text-fig. 130) ; the femur and genu are provided with one comb-like and two spatulate setae, respectively. The chelicera is shown in Text-fig. 131. The corniculus is distinctly stalked. Almost the entire lateral margins of the hypostomal processes are fringed. The deutosternal denticles on the ventral groove of the gnathosoma are shown in Text-fig. 132.

The tibia, tarsus and prae-tarsus of leg I are 121–150μ, 150–210μ and 17–25μ long respectively. The armature of the femur, genu, tibia and tarsus of leg II is of special interest (Plate 2g). The femur is strongly crassate and has a large falcate main spur and an accessory spur. The trochanter of leg IV is armed with a tubercle (Text-fig. 133).

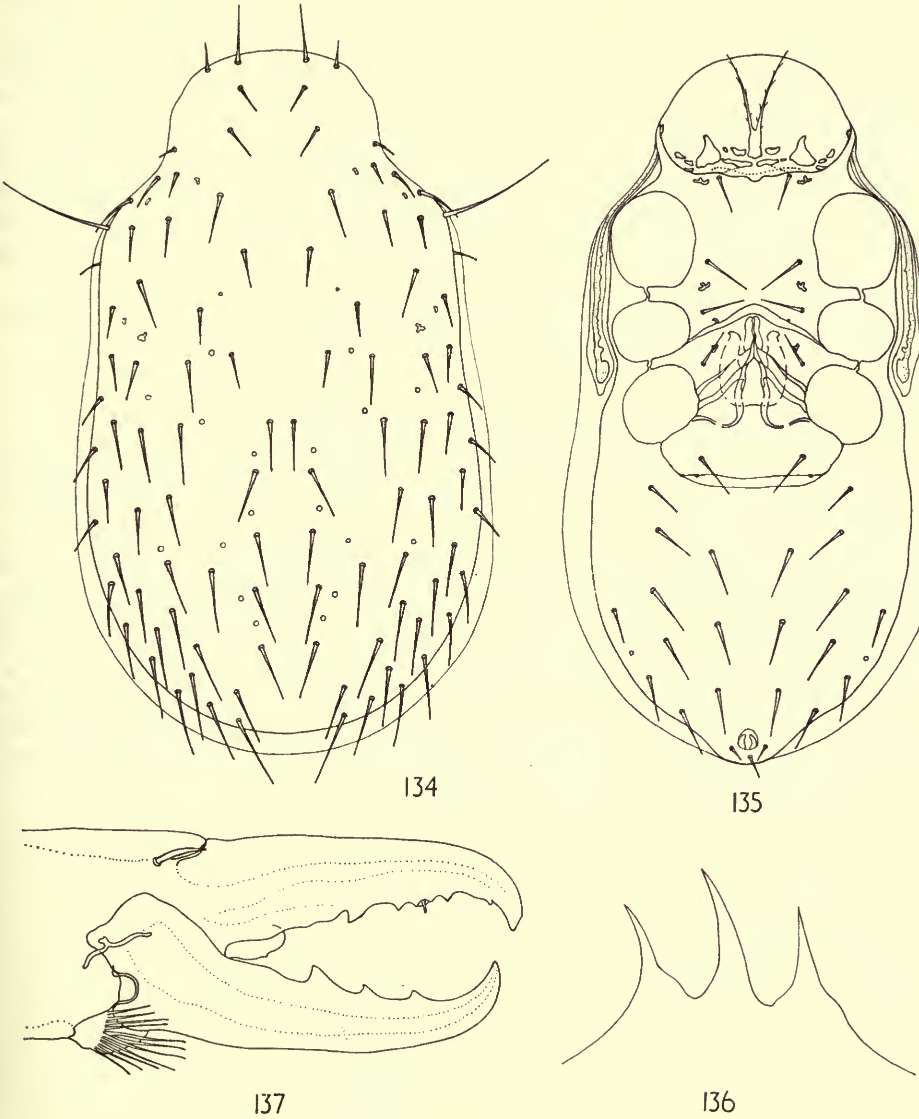
FEMALE. The dorsal shield (882–898μ long × 467–500μ wide) is well sclerotized and not entirely reticulated. The anterior half of the dorsal shield as usual bears twenty-one pairs of setae, and the posterior half is with twenty-nine pairs (Text-fig. 134).

Ventrally, the tritosternum has an elongated basal part, and a pair of ciliated laciniae. There are several pairs of prae-endopodal shields some of which are small. The interscutal membrane, between the anterior margin of the sternal shield and the prae-endopodal shields, is striated (Text-fig. 135). The endogynium consists of a pair of horns. The genital shield is shown in Plate 8c. The opisthogastral shield has ten pairs of setae (excepting a post-anal and a pair of paranal setae). The stigma is situated between the coxae III and IV, and the peritreme extends to the level of coxa I.

The tectum is three-pronged (Text-fig. 136). The distinctive features of the pedipalp are the femur with a comb-like seta and the genu with spatulate setae. The



FIGS. 127–133. *Pergamasus* (*Paragamasus*) *armatus* Halbert, male.
Fig. 127 dorsum of idiosoma. Fig. 128 venter. Fig. 129 tectum. Fig. 130 trochanter of pedipalp. Fig. 131 chelicera. Fig. 132 venter of gnathosoma. Fig. 133 trochanter of leg IV.



FIGS. 134–137. *Pergamasus* (*Paragamasus*) *armatus* Halbert, female. Fig. 134 dorsum of idiosoma. Fig. 135 venter. Fig. 136 tectum. Fig. 137 chelicera.

proximal half of the hypostomal process is fringed. The chelicera is as figured (Text-fig. 137).

The tibia, tarsus and prae-tarsus of leg I are 116–150μ, 154–183μ and 8–17μ long respectively. The trochanter of leg IV is without a tubercle.

Distribution and habitat. The female of the species is previously known from Ireland only (Halbert, 1915).

I have examined material from : hornbeam humus (Bookham Common, Surrey, Mrs. R. E. Teagle, xi.1956). In oak and beech leaf mould (Grasmere, Westmorland, J. T. Salmon, 26.vi.1951). Algae and rushes (Colletts Bridge, Norfolk, P. N. Lawrence, 16.x.1960). In beech leaf mould from steep bank (Rickmansworth, Herts., M. E. Bacchus, 25.ii.1951). Beech leaf mould (Amersham, Buckinghamshire, M. E. Bacchus, 13.v.1951). Inside bark of fallen elm tree (Harefield, Middlesex, A. H. G. Alston, 22.i.1956). Rotten reeds (Colletts Bridge, Norfolk, P. N. Lawrence).

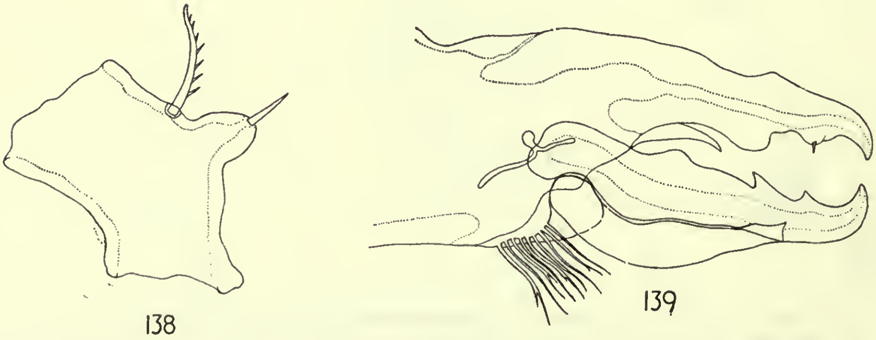
Moss on trees and humus (Hen Parc Wood, Killay nr. River Clyne, nr. Swansea, Wales, P. N. Lawrence, 24.iii.1962).

Pergamasus* (*Paragamasus*) *cambriensis sp. nov.

Male. The dorsal shield measures 490–500μ long × 240–250μ wide and is provided with a transverse suture. The anterior region of the dorsal shield bears twenty-one pairs of setae.

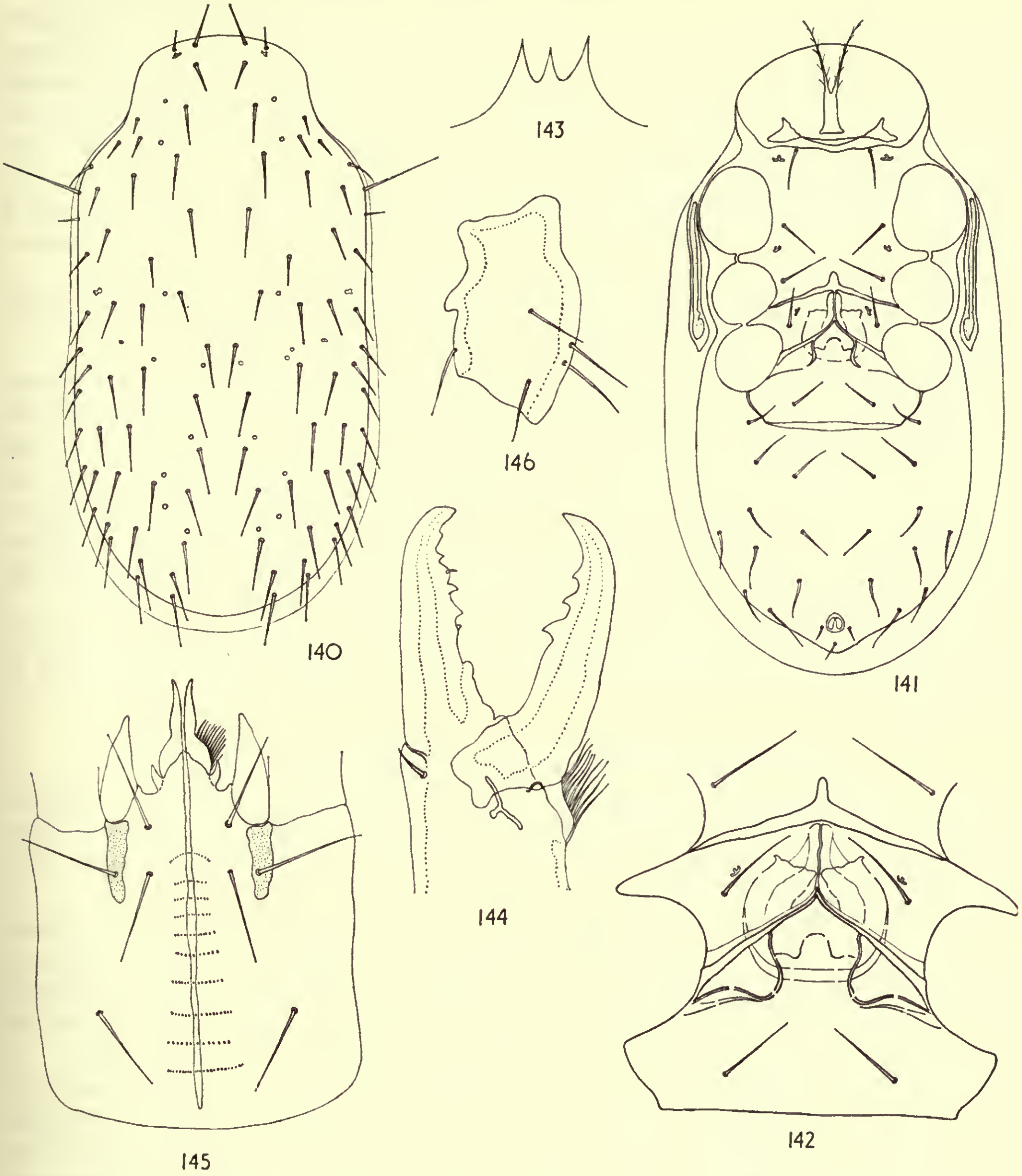
The tritosternum has a short basal part with a pair of pilose laciniae. A pair of large prae-endopodal shields is present. The genital lamina resembles that of *P. wasmanni* Oudemans. The stigma is situated between coxae III and IV ; and the peritreme extends to coxa II. A pair of post-stigmatal setae is present.

The tectum is three-pronged, the median tine being shorter than the lateral ones. The palpal trochanter has a seta-bearing tubercle (Text-fig. 138). The chelicera is shown in Text-fig. 139. The corniculus is distinctly stalked, and the entire lateral margins of the hypostomal processes are fringed.



Figs. 138–139. *Pergamasus* (*Paragamasus*) *cambriensis* sp. nov., male. Fig. 138 trochanter of pedipalp. Fig. 139 chelicera.

Leg I with the tibia, tarsus and prae-tarsus 66–70μ, 116–129μ and 8–12μ long, respectively. The femur, genu and tibia of leg II are armed with spurs (Plate 3a). The genual spur is characteristic in shape and position. The trochanter of leg IV is tuberculated.



FIGS. 140–146. *Pergamasus* (*Paragamasus*) *cambriensis* sp. nov., female. Fig. 140 dorsum of idiosoma. Fig. 141 venter. Fig. 142 magnified structure of the sterniti-genital region. Fig. 143 tectum. Fig. 144 chelicera. Fig. 145 venter of gnathosoma. Fig. 146 trochanter of leg IV.

FEMALE. The dorsal shield (515–548µ long × 267–300µ wide) is sclerotized and yellow in colour. The setation of the dorsal shield is shown in Text-fig. 140.

The tritosternum has an elongated basal part and a pair of pilose laciniae. A narrow elongated strip of prae-endopodal shield is situated in between large prae-endopodal shields (Text-fig. 141). The metasternal shields are free. The genital region is as in Text-fig. 142, and the genital shield in Plate 8d. The opisthogastral shield with ten pairs of setae. Although the peritrematal shield is fused with the dorsal shield at the level of coxa I the peritreme only extends to coxa II. The position of the stigma is the same as in the male.

The tectum is three-pronged (Text-fig. 143). The dentition of the chelicera is shown in Text-fig. 144. The deutosternal denticles are arranged in ten transverse rows.

Leg I with the tibia, tarsus and prae-tarsus 78–87μ, 125–137μ and 8–12μ long respectively. The trochanter of leg IV is shown in Text-fig. 146.

HABITAT. Two males and three females from hornbeam humus (Bookham Common, Surrey, Mrs. R. E. Teagle, xi.1956), two females from beech leaf mould (Amersham, Buckinghamshire, M. E. Bacchus, 13.v.1951). Three females in soil (between Rockingham and Corby, Northants, B. N. K. Davis, 14.i.1958). Six males and thirteen females from litter under thick evergreen hedge (St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 29.iii.1957). Two females from pine litter (Clyne Park, Swansea, S. K. Bhattacharyya, 4.i.1961). Two females from oak litter (Llew Reservoir, Swansea, S. K. Bhattacharyya, 2.i.1961).

I have designated a male and female from Bookham Common, Surrey (Coll. Mrs. R. E. Teagle, xi.1956) as the Holotype (1963.2.7.1) and Allotype (1963.2.7.2) respectively.

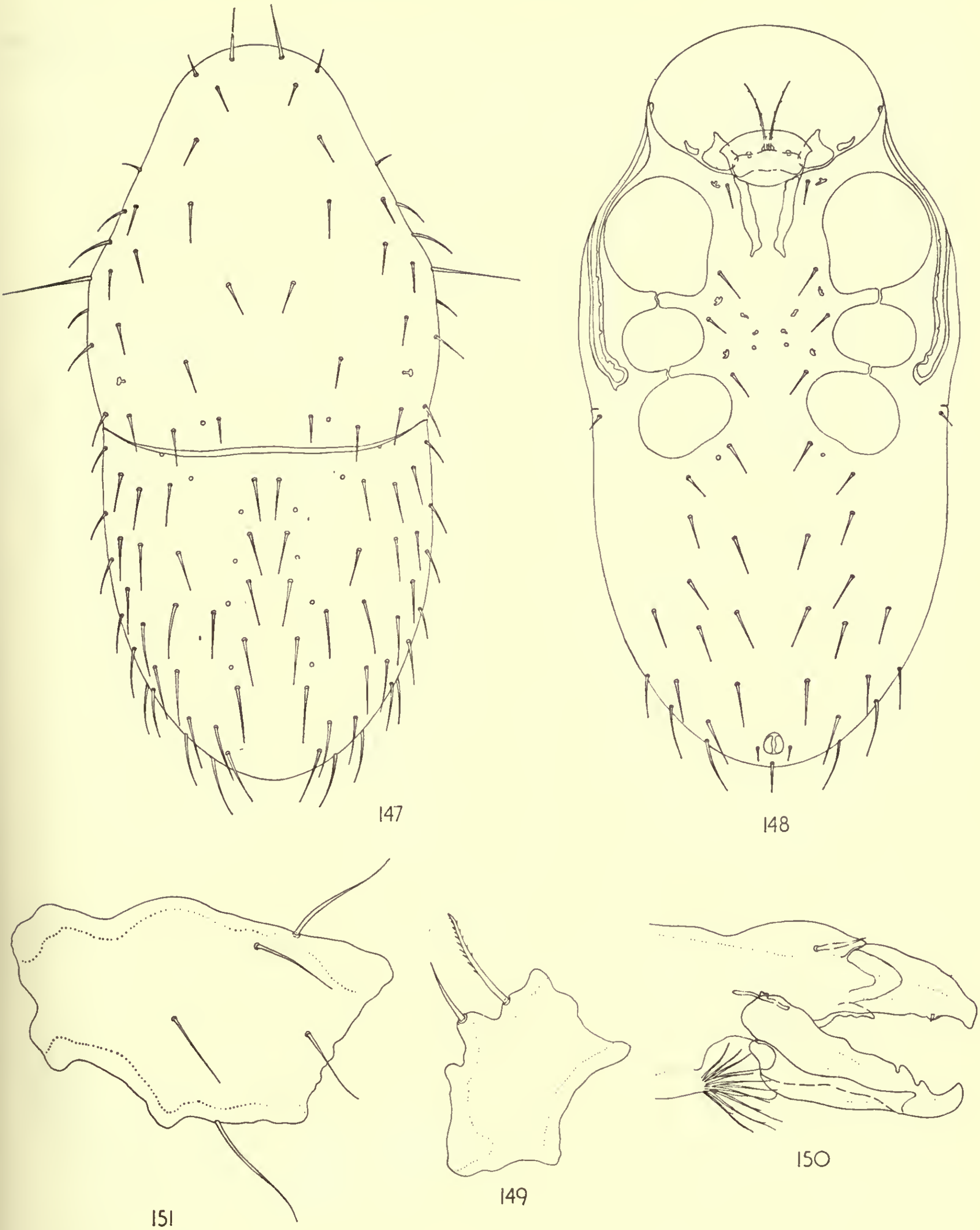
Pergamasus (Paragamasus) cassiteridum sp. nov.

MALE. This species is strongly sclerotized and dark brown in colour. The dorsal shield (86–88μ long × 433–467μ wide) has a transverse suture (Text-fig. 147). The anterior dorsal shield bears twenty-one pairs of setae, whilst the posterior half about twenty-six pairs of setae.

The tritosternum has a reduced base with a pair of pilose laciniae. The anterior-most margin of the genital lamina is convex in shape. The distribution of the prae-endopodal shields and the setation of the opisthogastral shield is shown in Text-fig. 148. The stigma is situated between coxae III and IV ; the peritreme anteriorly extends as far as the level of coxa I. A pair of post-stigmatal setae is present.

The tectum is three-pronged. The most distinctive features of the pedipalp are, the trochanter with two tubercles (Text-fig. 149), the femur with a comb-like seta and the genu with two spatulate setae. The dentition of the chelicera and the form of the spermadactyl process is shown in Text-fig. 150. There are distinctly stalked corniculi. The entire lateral margins of the hypostomal processes are fringed.

The tibia, tarsus and prae-tarsus of leg I are 121–129μ, 145–154μ and 17μ long respectively. The trochanter, femur and genu of leg II are armed with variously shaped processes (Plate 3c–e). The femur is crassate. The tibial spur is smaller than in *robustus* and the distal end has a prominence. The armature of the trochanter of leg IV is delineated in Text-fig. 151.

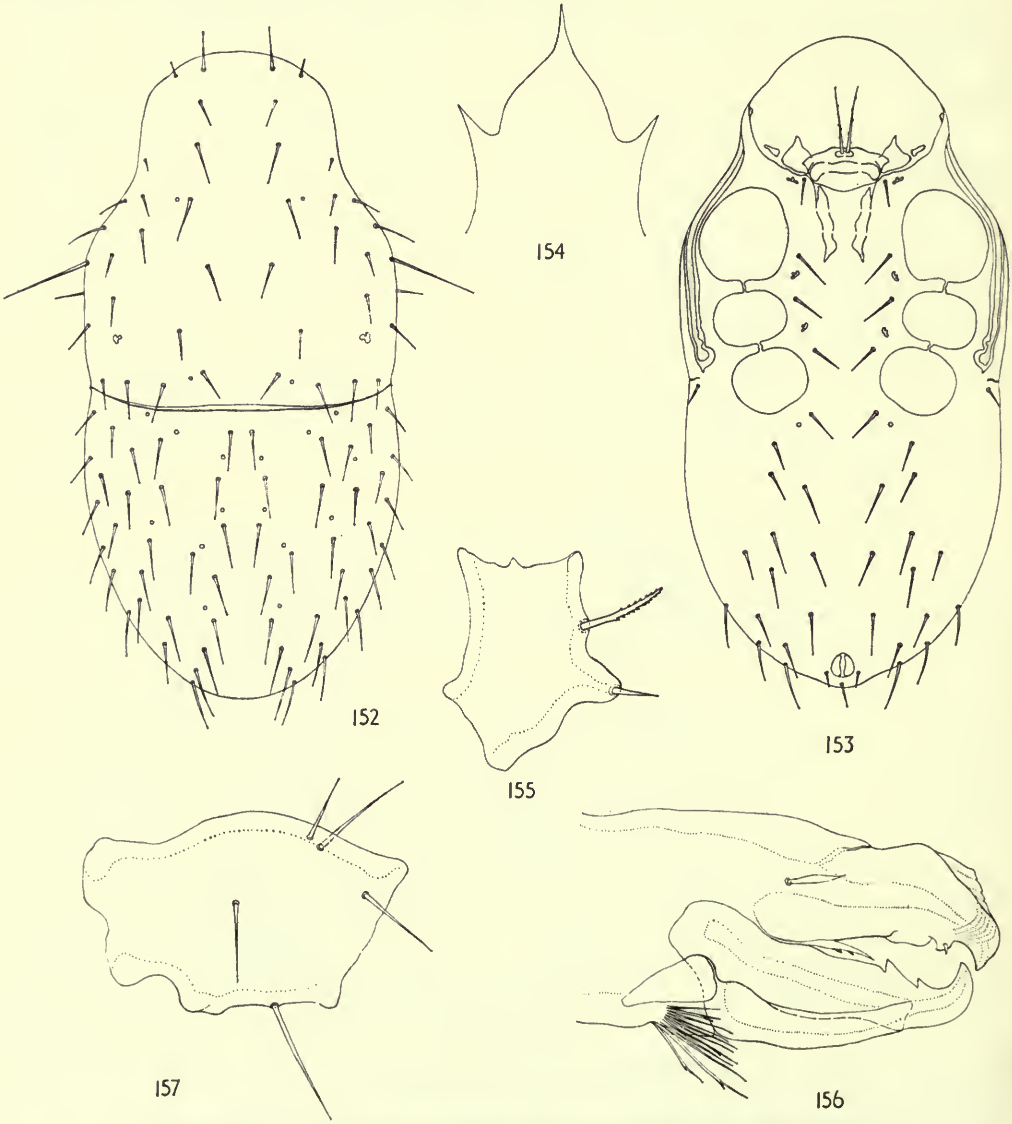


FIGS. 147–151. *Pergamasus* (*Paragamasus*) *cassiteridum* sp. nov., male. Fig. 147 dorsum of idiosoma. Fig. 148 venter. Fig. 149 trochanter of pedipalp. Fig. 150 chelicera. Fig. 151 trochanter of leg IV.

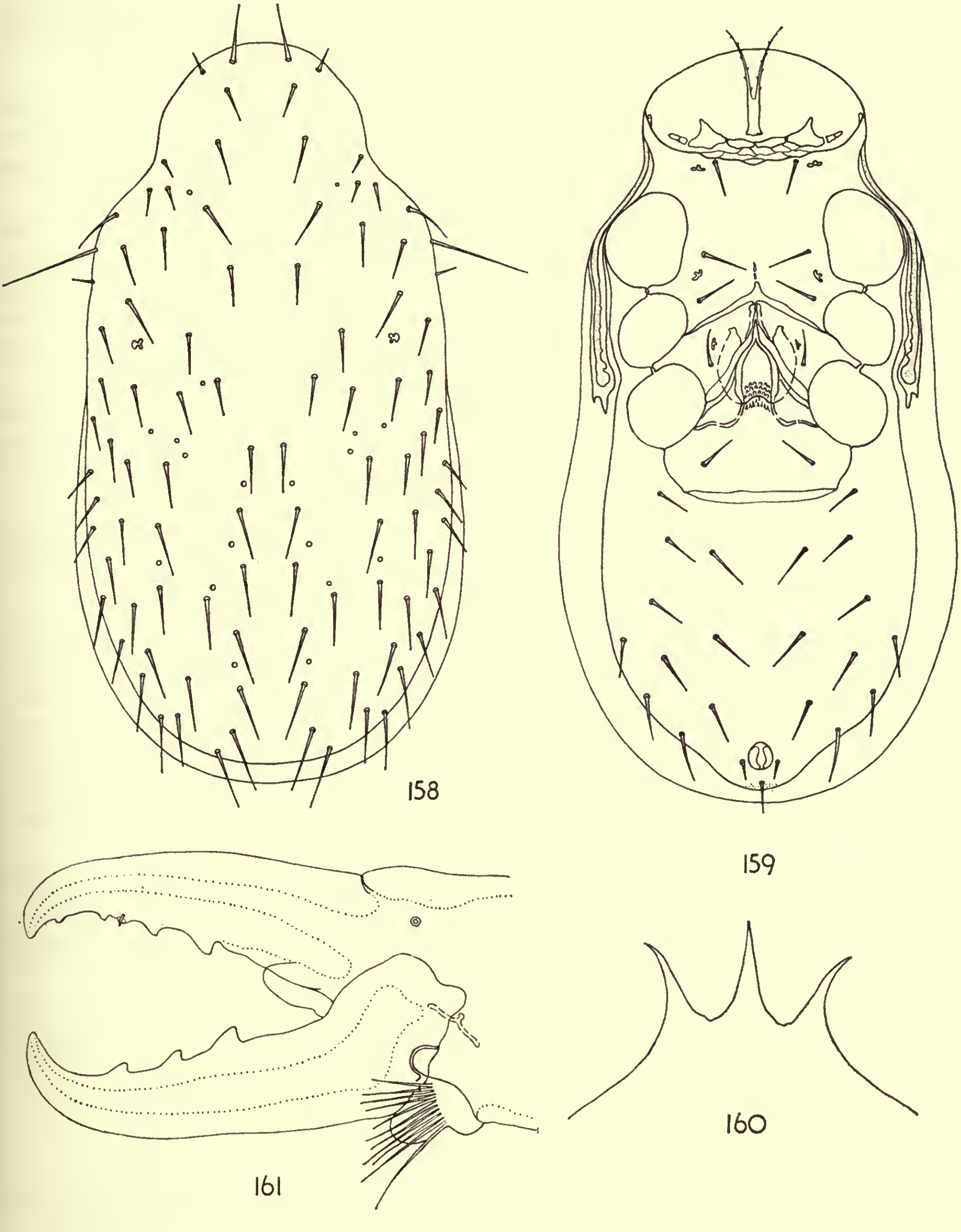
FEMALE. Unknown.

HABITAT. One male from litter under thick evergreen hedge, St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 29.iii.1957, and two males from lichens in crevices, Moel Siabod, North Wales, P. N. Lawrence, 22.x.1960.

I have designated the male from St. Agnes, Isles of Scilly, Cornwall (Coll. K. H. Hyatt, 29.iii.1957) as the Holotype (1963.2.7.7).



FIGS. 152–157 *Pergamasus* (*Paragamasus*) *celticus* sp. nov., male. Fig. 152 dorsum of idiosoma. Fig. 153 venter. Fig. 154 tectum. Fig. 155 trochanter of pedipalp. Fig. 156 chelicera. Fig. 157 trochanter of leg IV.



FIGS. 158-161. *Pergamasus* (*Paragamasus*) *celticus* sp. nov., female.
Fig. 158 dorsum of idiosoma. Fig. 159 venter. Fig. 160 tectum. Fig. 161 chelicera.

Pergamasus (Paragamasus) celticus sp. nov.

MALE. The dorsal shield measures 732–747μ long and 367μ wide and is provided with a transverse suture (Text-fig. 152). The dorsum bears about forty-nine pairs of setae of which twenty-one pairs are situated on the anterior dorsal shield.

Ventrally, the tritosternum has a pair of pilose laciniae. The distribution of the prae-endopodal shields and the shape of the genital lamina are shown in Text-fig. 153. The stigma is situated between coxae II and IV and the peritreme reaches to coxa I. A pair of post-stigmatal setae is present.

The tectum is three-pronged (Text-fig. 154). The distinctive features of the pedipalp are, the trochanter has a seta-bearing process (Text-fig. 155), the femur a comb-like seta and the genu two spatulate setae. The characteristic shape of the fixed digit and the dentition of the chelicera are shown in Text-fig. 156. The corniculus is distinctly stalked. The entire lateral margins of the hypostomal processes are fringed.

Leg I is with the tibia, tarsus and prae-tarsus 100–133μ, 168–175μ and 16–21μ long, respectively. The trochanter of leg II lacks a spur but the femur, genu and tibia are armed with variously shaped processes (Plate 3g). The trochanter of leg IV is shown in Text-fig. 157.

FEMALE. The dorsal shield (704–732μ long × 357–374μ wide) is well sclerotized and yellow in colour. The podonotal shield invariably bears twenty-one pairs of setae but the opisthonotal shield has about twenty-seven pairs (Text-fig. 158).

The tritosternum has an elongated basal part and a pair of pilose laciniae. The form of the prae-endopodal shield is shown in Text-fig. 159. Ventro-medially, the interscutal membrane between the anterior margin of the sternal and prae-endopodal shields is striated and granular. The metasternal shields are free. The endogynium has a pair of horns and its processes are delineated in Text-fig. 159. The epigynial shield is shown in Plate 8f. The opisthonotal shield is with ten pairs of setae. The position of the stigma and extension of the peritreme are similar to those in the male.

The tectum is three-pronged (Text-fig. 160). The chelicera is shown in Text-fig. 161. The ventral groove of the gnathosoma has nine or ten rows of denticles.

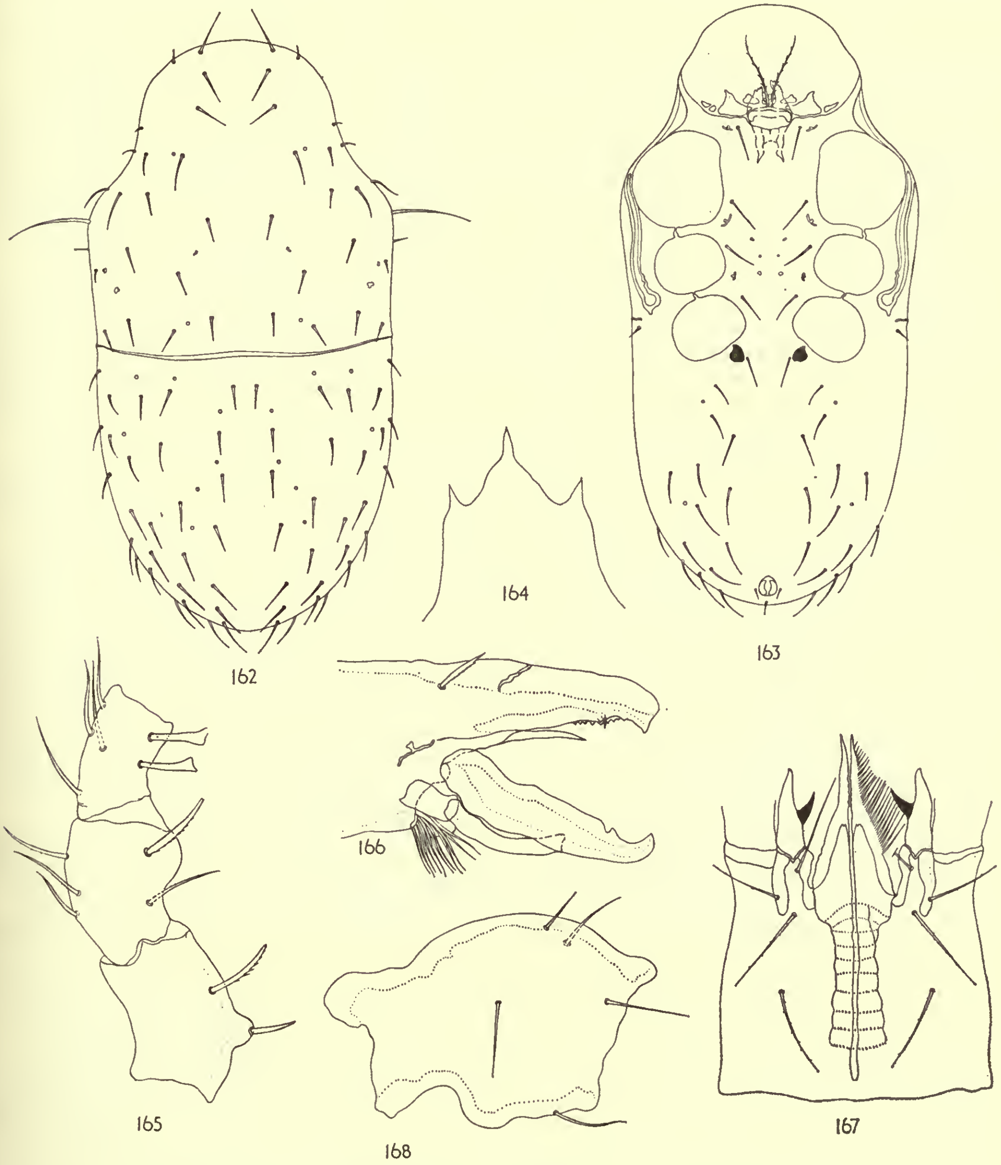
The tibia, tarsus and prae-tarsus of leg I are 112μ, 133–185μ and 10–12μ long, respectively. The trochanter of leg IV is without any process.

HABITAT. Three males and four females have been obtained from pines and rhododendrons (Parknasilla, Co. Kerry, Ireland, Miss T. Clay, 27.i.1953); Holotype male (1963.2.7.17) and Allotype female (1963.2.7.18).

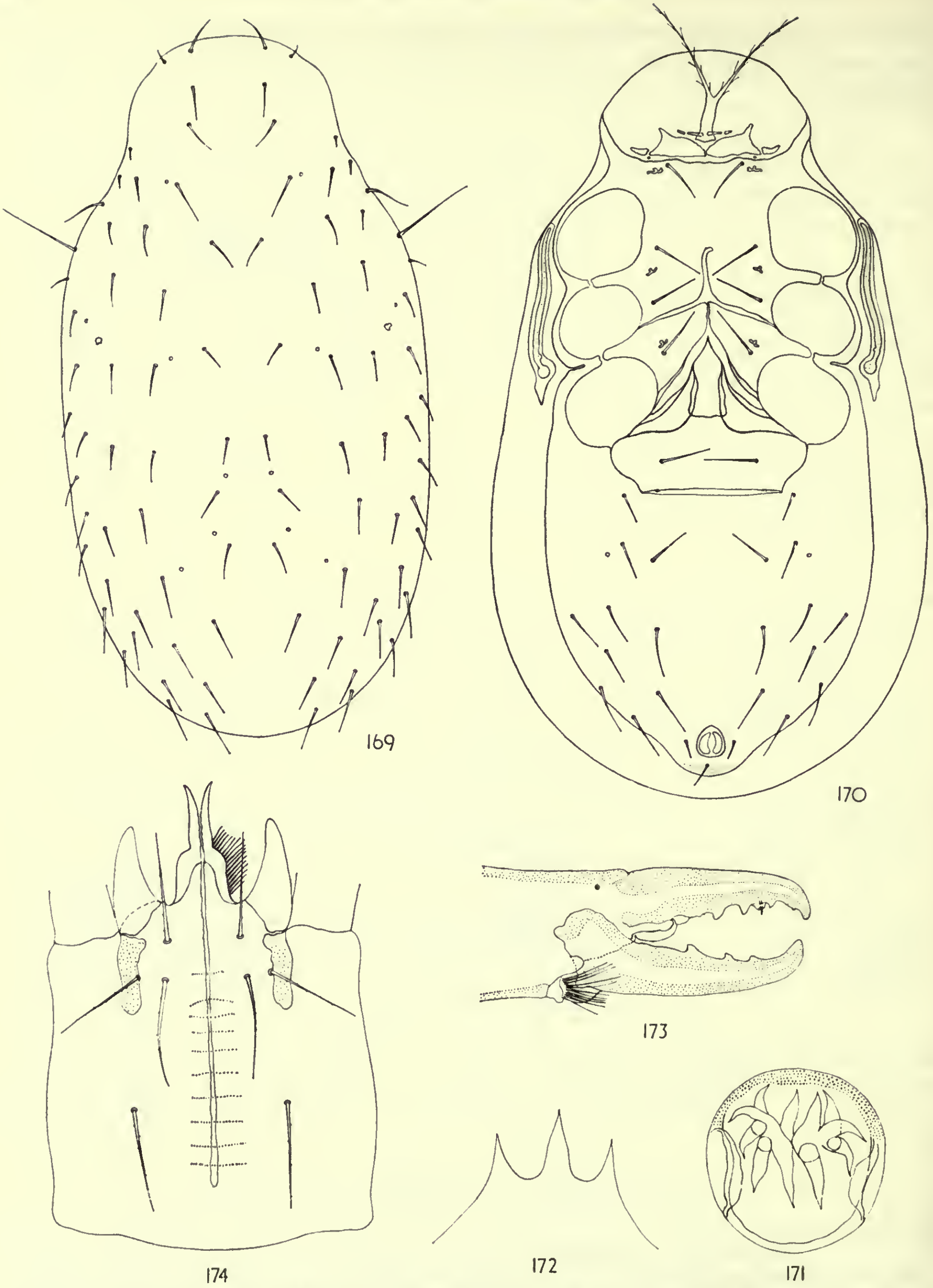
Pergamasus (Paragamasus) diversus Halbert

Gamasus (Pergamasus) diversus Halbert, J. N. (1915). *Proc. R. Irish Acad.* **31** 39 ii : **52**, figs.

MALE. The dorsal shield (831–898μ long × 400–440μ wide) is well sclerotized and provided with a transverse suture (Text-fig. 162). The anterior region of the dorsal shield is furnished with twenty-one pairs of setae and is regionally reticulated. The posterior region of the shield bears twenty-five pairs of setae and is entirely reticulated.



Figs. 162–168. *Pergamasus* (*Paragamasus*) *diversus* Halbert, male.
Fig. 162 dorsum of idiosoma. Fig. 163 venter. Fig. 164 tectum. Fig. 165 trochanter, femur and genu of pedipalp. Fig. 166 chelicera. Fig. 167 venter of gnathosoma. Fig. 168 trochanter of leg IV.



Figs. 169–174. *Pergamasus* (*Paragamasus*) *diversus* Halbert, female. Fig. 169 dorsum of idiosoma. Fig. 170 venter. Fig. 171 endogynial process. Fig. 172 tectum. Fig. 173 chelicera. Fig. 174 venter of gnathosoma.

The tritosternum has a short basal part and a pair of pilose laciniae. The genital lamina is medially notched into two lobes which have serrated margins (Text-fig. 163). Between coxae IV are a pair of well sclerotized, scale-like structures. Each scale-like structure is associated with a seta. The stigma is situated between coxae III and IV ; the peritreme extends to coxa II. A pair of post-stigmatal setae is present.

The tectum is three-pronged (Text-fig. 164). The palpal trochanter has a seta-bearing process ; the femur and genu are provided with a comb-like and two spatulate setae respectively (Text-fig. 165). The chelicera is shown in Text-fig. 166. The corniculus is stalked and provided with a blade-like hyaline appendage (Text-fig. 167). The hypostomal process and deutosternal denticles are shown in the figure.

The tibia, tarsus and prae-tarsus of leg I are 125–158μ, 191–213μ and 12–17μ long, respectively. The femur of leg II is crassate with a strong falcate main spur and an accessory spur. The distal end of the femur also bears a tubular process. The genu lacks a process ; whilst the tibia bears a discoidal spur (Plate 3b). The trochanter of leg IV is shown in Text-fig. 168.

Female. The dorsal shield (831–847μ long × 433–450μ wide) is sclerotized. The anterior region of the dorsal shield has twenty-one pairs of setae and the posterior region about twenty-four pairs (Text-fig. 169).

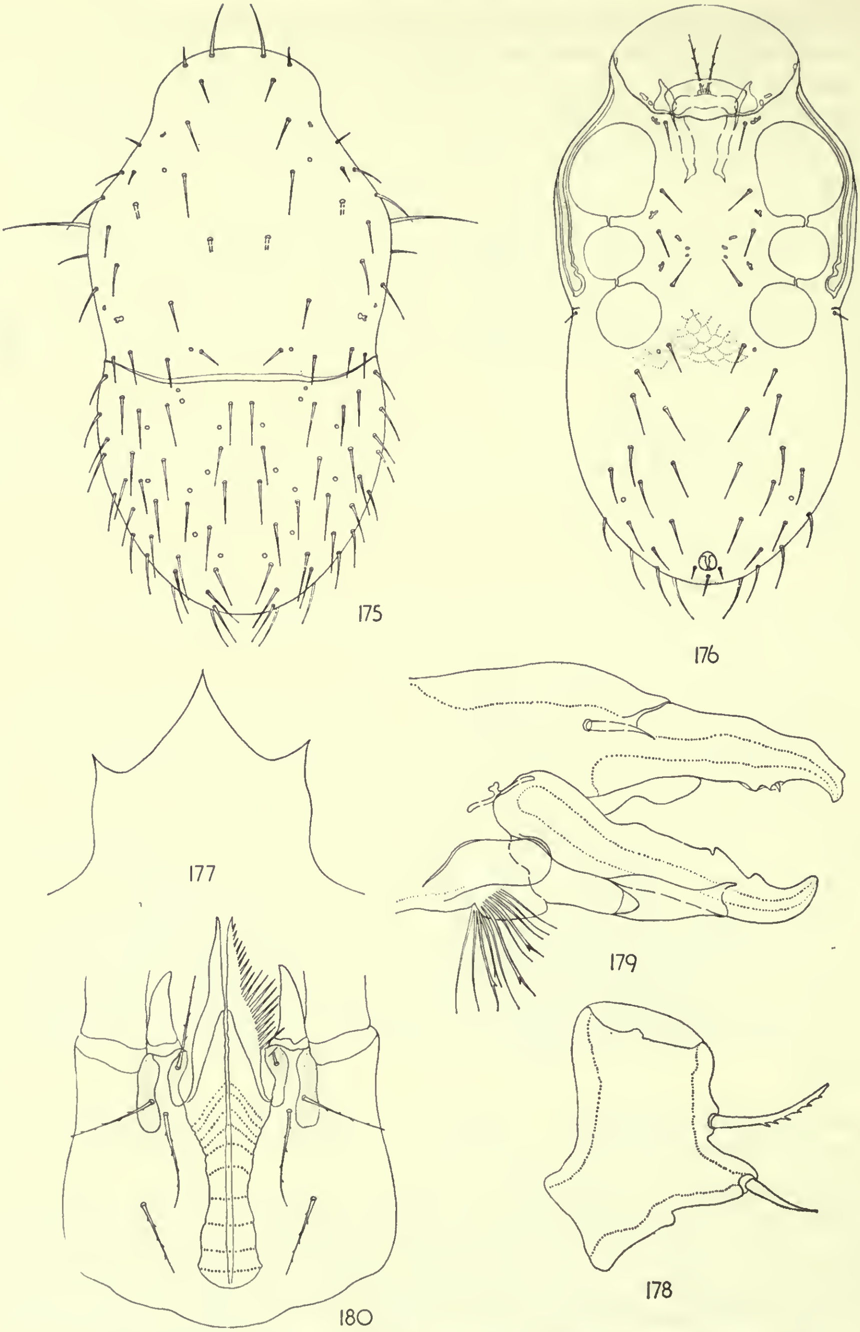
The tritosternum has a well developed basal part. The distribution of the prae-endopodal shields is shown in Text-fig. 170. The posterior margin of the sternal shield has a median incision which extends to the level of the second pair of sternal setae. The metasternal shields are free and flank the epigynial shield. A pair of endogynial horns is present. The complicated endogynial processes are figured (Text-fig. 171). The genital shield is shown in Plate 7h. The opisthogastric shield bears ten pairs of setae (excepting three setae associated with the anus). The position of the stigma and the extension of the peritreme are similar to that in the male.

The tectum is three-pronged (Text-fig. 172). The palp is basically similar to that in the male. The dentition of the chelicera is shown in Text-fig. 173. The ventral groove of the gnathosoma has ten transverse rows of denticles (Text-fig. 174).

The tibia, tarsus and prae-tarsus of leg I are 121–145μ, 170–191μ and 8–17μ long, respectively.

Distribution and habitat. The male of this species has previously been recorded only from Ireland (Halbert, 1915).

I have examined specimens from : litter and soil under evergreen trees (St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 5.iv.1957). In leaf mould (Rye, Houghton Green, Sussex, J. T. Salmon, 19.v.1951). Rotten wood (Blurridge Farm, Ridge Hill, Combe Martin, Devonshire, M. E. Bacchus, 12.iii.1957). *Salix* sp. litter (British Museum (Nat. Hist.), London, S. K. Bhattacharyya, 5.iii.1962). Rotten reeds (Colletts Bridge, Norfolk, P. N. Lawrence). Litter under thick evergreen hedge (St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 29.iii.1957). Pine litter (Clyne Park, Swansea, S. K. Bhattacharyya, 4.i.1961). Moss humus



FIGS. 175–180. *Pergamasus* (*Paragamasus*) *femoratus* sp. nov., male.
Fig. 175 dorsum of idiosoma. Fig. 176 venter. Fig. 177 tectum. Fig. 178 trochanter of pedipalp. Fig. 179 chelicera. Fig. 180 venter of gnathosoma.

and humus in small wood (Swansea University, Swansea, P. N. Lawrence, 26.iii.1962). Moss on trees and humus (Hen Parc Wood, Killay, nr. River Clyne, Swansea, P. N. Lawrence, 24.iii.1962). Oak and beech litter (Singleton Park, Swansea, S. K. Bhattacharyya, 3.i.1961). Under pines and rhododendrons (Parknasilla, Co. Kerry, Ireland, Miss T. Clay, 27.i.1953).

Pergamasus (Paragamasus) femoratus sp. nov.

MALE. The dorsal shield (854μ long × 440μ wide) is moderately sclerotized and provided with a transverse suture (Text-fig. 175). The anterior dorsal shield has twenty-one pairs of setae and the posterior dorsal shield about twenty-six pairs.

Ventrally, the tritosternal base and the proximal part of the pilose laciniae are covered by the genital lamina. The distribution of the prae-endopodal shields and the setation of the opisthogastral shield are shown in Text-fig. 176. The stigma is situated between coxae III and IV with the extension of the peritreme to coxa I.

The tectum is three-pointed (Text-fig. 177). The palpal trochanter is shown in Text-fig. 178. The femur and genu is with one comb-like and two spatulate setae respectively. The characteristic features of the chelicera are shown in Text-fig. 179. The corniculus, hypostomal process and rows of deutosternal denticles are figured (Text-fig. 180).

The tibia, tarsus and prae-tarsus of leg I are 145μ, 200–204μ and 41μ long, respectively. The femur, genu and tibia of leg II are armed with variously shaped processes (Plate 4a). The femur is characterized by the presence of a tubular spur near the proximal end of the segment, thus the name *femoratus*. The trochanter of leg IV lacks a tubercle.

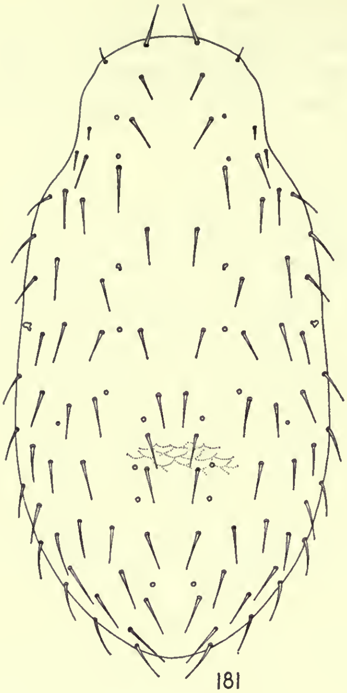
HABITAT. I have examined a single male (Holotype 1963.2.7.12) from mosses on rocks (Ballyporty Loughs, Co. Clare, Ireland, Coll. P. N. Lawrence, 12.vii.1960).

Pergamasus (Paragamasus) integer sp. nov.

MALE. This species is reddish-brown in colour, well sclerotized and regionally reticulated. The dorsal shield (747μ long × 389μ wide) has no transverse suture (Text-fig. 181). It usually bears forty-six pairs of setae of which twenty pairs are situated on the anterior half of the dorsal shield. The number of setae varies on the posterior half of the dorsal shield.

The tritosternum has a pair of pilose laciniae and its base is hidden by the genital sclerite. The distribution of the prae-endopodal shields is shown in Text-fig. 182. The setation of the opisthogastral shield is as figured. The stigma is situated between coxae III and IV ; the peritreme extends to coxa I. A pair of post-stigmatal setae, one on each side, is present.

The tectum is as figured with three prongs, of which the median is much longer and broader based (Text-fig. 183). The palpal trochanter is shown in Text-fig. 184 ; a comb-like seta is present on the femur and the genu carries two spatulate setae. The fixed digit of the chelicera has a row of closely-set teeth and a simple



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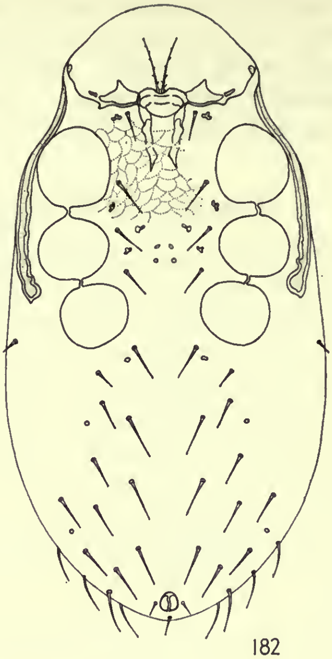

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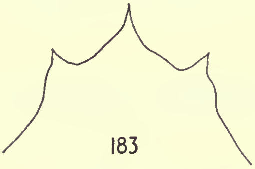

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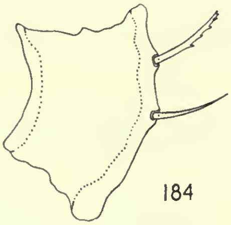

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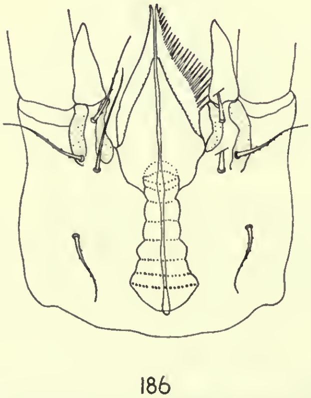

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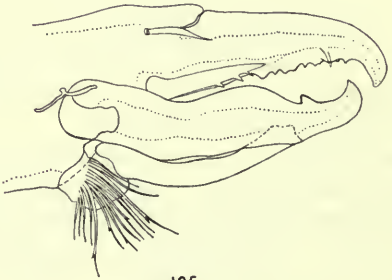

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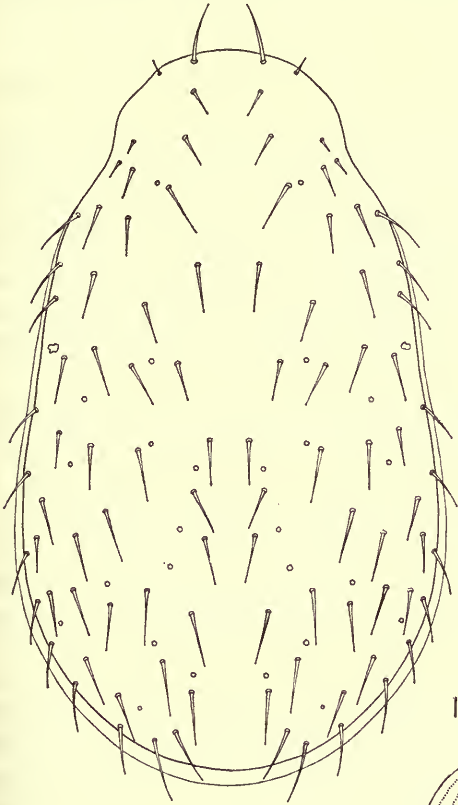
FIGS. 181–186. *Pergamasus* (*Paragamasus*) *integer* sp. nov., male.
Fig. 181 dorsum of idiosoma. Fig. 182 venter. Fig. 183 tectum. Fig. 184 trochanter of pedipalp. Fig. 185 chelicera. Fig. 186 venter of gnathosoma.

dorsal seta. The movable digit is unidentate and shorter than the fixed digit (Text-fig. 185). The spermadactyl is normal. The corniculus is stalked. The entire lateral margins of the hypostomal processes are fringed. The deutosternal



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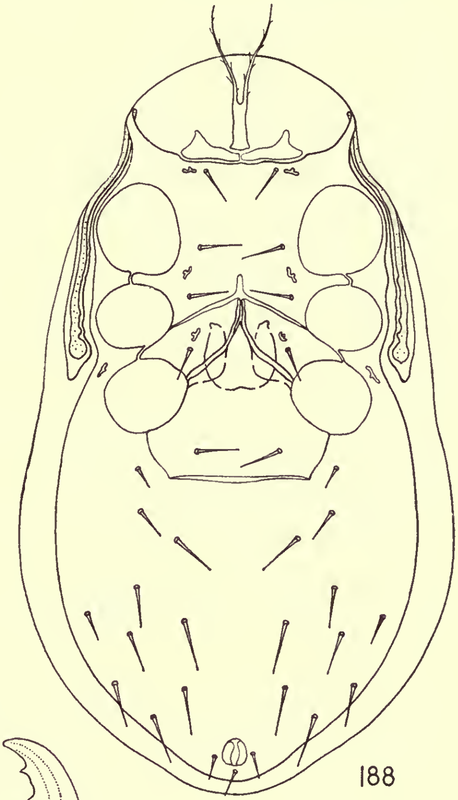

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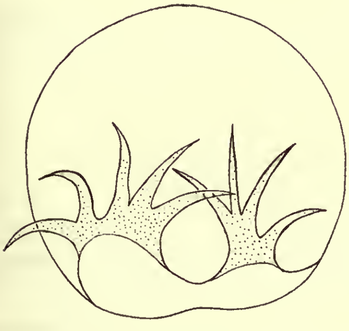

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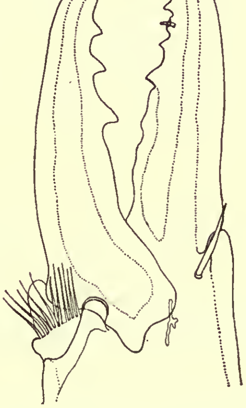

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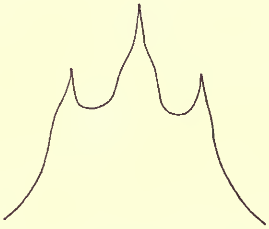

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Figs. 187–191. *Pergamasus* (*Paragamasus*) *integer* sp. nov., female.
Fig. 187 dorsum of idiosoma. Fig. 188 venter. Fig. 189 endogynial process. Fig. 190 tectum. Fig. 191 chelicera.

denticles are arranged in ten transverse rows (Text-fig. 186). The hypostome bears the usual four pairs of setae of which three pairs are distinctly pilose.

The tibia, tarsus and prae-tarsus of leg I are 116–121μ, 183–187μ and 17μ long, respectively. The distinctive features of leg II are delineated in Plate 4b. The trochanter of leg IV is as drawn simple.

FEMALE. The dorsal shield (889–967μ long × 500–565μ wide) is well sclerotized and its setation shown in Text-fig. 187.

Ventrally, the tritosternum has an elongated basal part and a pair of pilose laciniae. A pair of large prae-endopodal shields is present (Text-fig. 188). The metasternal shields are free. The endogynium has a pair of horns. The endogynial process is shown in Text-fig. 189. The genital shield is shown in Plate 7i. The opisthogastral shield bears ten pairs of setae (excepting three setae associated with the anus). The stigma lies between coxae III and IV ; and the peritreme extends to coxa I. The peritrematal shield runs for a short distance as a post-stigmatal prolongation.

The tectum is three-pronged, the median prong being in advance of the lateral ones (Text-fig. 190). The pedipalp essentially resembles that of the male. The chelicera is as figured (Text-fig. 191).

The tibia, tarsus and prae-tarsus of leg I are 125–129μ, 208–215μ and 17–21μ long respectively. The trochanter of leg IV is without a special prominence.

HABITAT. I have examined two males and two females from moss on trees and humus (Hen Parc Wood, Killay nr. River Clyne, nr. Swansea, P. N. Lawrence, 24.iii.1962).

One female in leaf mould (Boltons Wood, Boltons Abbey, North Riding, Yorkshire, J. T. Salmon, 24.vi.1951). Two females in oak and beech leaf mould (Grasmere, Westmorland, J. T. Salmon, 26.vi.1951). Three females in rotten wood from *Pinus* sp. in woodland belt (near St. Catherines Castle, Fowey, Cornwall, Mrs. R. E. Teagle, ii.1957). Nine females and one male in moss on wall (Tarn Hows, N. Lancashire, M. E. Bacchus, 4.xii.1954).

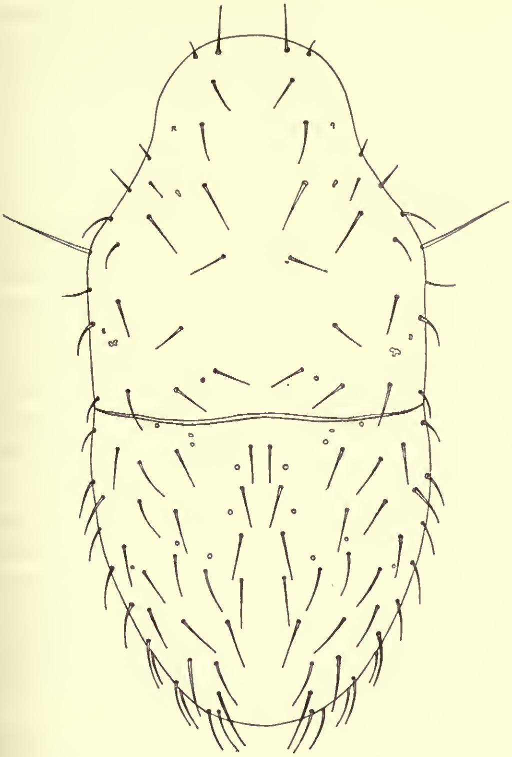
I have designated a male and female from Hen Parc Wood, Killay, nr. River Clyne, nr. Swansea, as the Holotype (1963.2.7.3) and Allotype (1963.2.7.6), respectively.

Pergamasus (Paragamasus) lapponicus Trägårdh

Pergamasus lapponicus Trägårdh, I. (1910). *Naturw. Untersuch. Sarekgeb.* **4** (4) : 408, figs. Cooreman, J. (1943). *Bull. Mus. roy. Hist. nat. Belg.*, **19**, 63 : 5, figs. ; Schweizer, J. (1949). *Ergebn. wissens. Untersuch. Schweiz. Nationalparkes* (n.s.) **2** : 28, figs ; Schweizer, J. (1961). *Denks. schweiz. naturf. Ges.* **84** : 56, figs.

MALE. The dorsal shield (797–831μ long × 400–417μ wide) has a transverse suture (Text-fig. 192) and is regionally reticulated. The anterior dorsal shield bears twenty-one pairs of setae and the posterior dorsal shield about twenty-eight pairs.

The tritosternum has a pair of pilose laciniae but its base is completely hidden by the genital sclerite. The shape of the genital lamina is shown in Text-fig. 193.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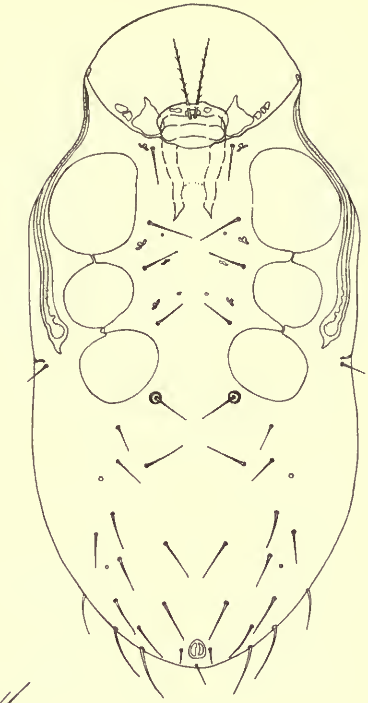
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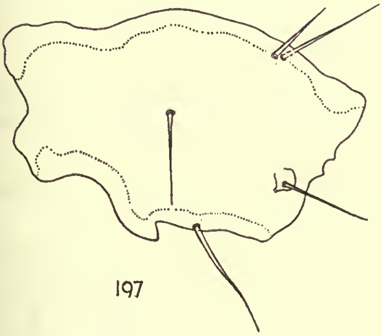
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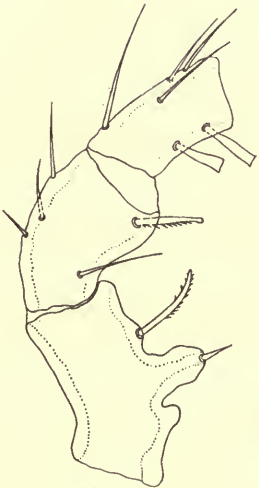
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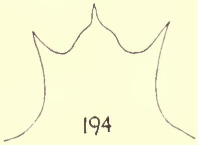
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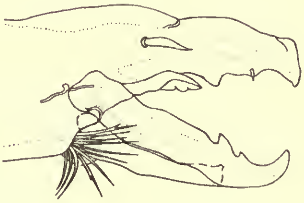
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FIGS. 192–197. *Pergamasus* (*Paragamasus*) *lapponicus* Trägårdh, male. Fig. 192 dorsum of idiosoma. Fig. 193 venter. Fig. 194 tectum. Fig. 195 trochanter, femur and genu of pedipalp. Fig. 196 chelicera. Fig. 197 trochanter of leg IV.

The venter has a remarkable rounded, scaly, seta-bearing structure near coxa IV. The number of setae on the opisthogastric shield is shown in Text-fig. 193. The stigma is situated between the coxae III and IV ; the peritreme extends to coxa I. There is a post-stigmatal seta.

The tectum is three-pointed (Text-fig. 194). The palpal trochanter has a modified nipple-like setae-bearing process, at the base of which is a small protuberance ; a comb-like seta is present on the femur whilst the genu has two spatulate setae (Text-fig. 195). The distinctive shape of the fixed digit of the chelicera is shown in Text-fig. 196. The movable digit is bidentate, and the spermadactyl is normal. The corniculus is distinctly stalked. The entire lateral (outer) margins of the hypostomal processes are fringed.

The tarsus (187–208μ) of leg I is longer than the tibia (141–145μ) ; the prae-tarsus is 17–21μ long. The trochanter (Plate 4c) of leg II has a well developed spur ; the femur, genu and tibia are spurred (Plate 4d). The main process of the crassate femur is falcate. The armature of the trochanter of leg IV is figured (Text-fig. 197).

FEMALE. The dorsal shield (764–797μ long × 400–467μ wide) is more or less oval and yellow in colour and regionally reticulated. The anterior shield has only twenty-one pairs of setae and the posterior half bears about twenty-nine pairs (Text-fig. 198). The length of the dorsal setae vary considerably.

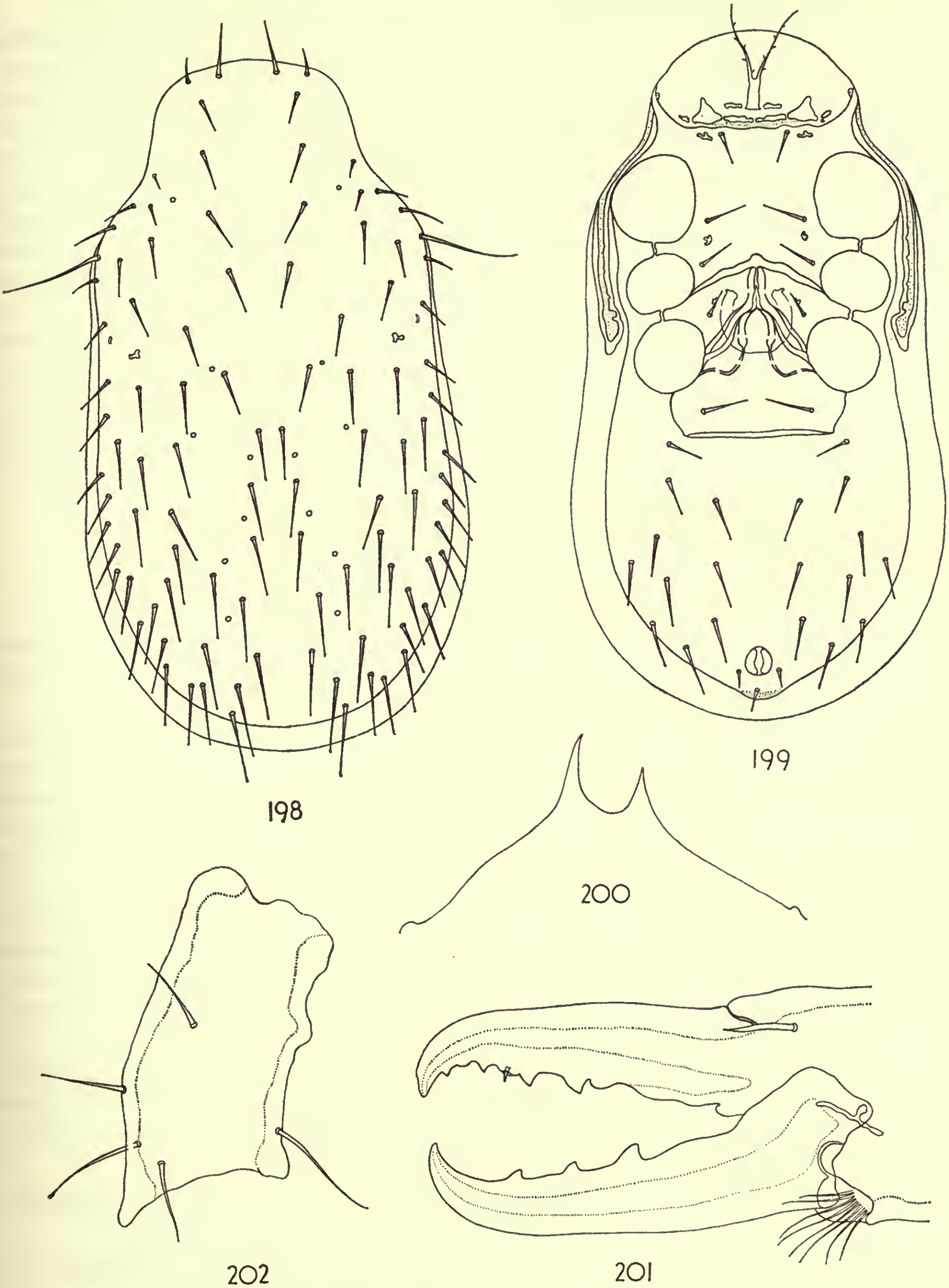
Ventrally, the tritosternum has a pair of well developed pilose laciniae. The distribution of the prae-endopodal shields is shown in Text-fig. 199. The interscutal membrane in between the anterior margin of the sternal shield and the prae-endopodal shield is striated. The metasternal shield is free. There is a pair of endogynial horns. The genital shields are shown in Plate 8h and i. The opisthogastral shield is with ten pairs of setae. The stigma is situated between coxae III and IV ; and the peritreme reaches to the level of coxa I.

The tectum is basically three pronged but may be variable (Text-fig. 200). The fixed digit of the chelicera has four teeth but the movable digit is tridentate (Text-fig. 201).

The tibia, tarsus and prae-tarsus of leg I are 137–141μ, 196–200μ and 16–18μ long, respectively. The trochanter of leg IV is figured (Text-fig. 202).

DISTRIBUTION AND HABITAT. This species is known from Swedish Lapland (Trägårdh, 1910), Belgium (Cooreman, 1943), Germany and Switzerland (Schweizer, 1949, 1961).

I have examined material from leaf mould (Epping Forest, Essex, J. T. Salmon, 27.v.1951). *Sphagnum*, etc. (Cock Hill, Yorkshire, J. T. Salmon, 21.vii.1951). In marsh debris (Surlingham, Norfolk, J. T. Salmon, 12.v.1951). In leaf mould (Savernake Forest, Berkshire, J. T. Salmon, 26.ix.1951). Litter and humus under pines and holly (near Duddleswell, Ashdown Forest, Sussex, K. H. Hyatt, 10.ix.1956). In leaf mould (Forest of Dean, Gloucestershire, J. T. Salmon, 27.ix.1951). From litter (Stratton Strawless, near Aylsham, Norwich, Norfolk, J. T. Salmon, 13.v.1951). In moss of wall (Tarn Hows, North Lancashire, M. E. Bacchus, 4.xii.1954). In moss (Grassington, Grass Woods, North Riding, Yorkshire, J. T. Salmon, 24.vi.1951). In *Sphagnum* (Virginia Water, Surrey, A. H. G. Alston, 18.xii.1951). *Sphagnum* (Ascot, Berkshire, A. H. G. Alston, 8.xii.1957). Moles' (*Talpa europaea*) nest, near pasture (Godstone, Surrey, Prof. P. A. Larkin, 4.xi.1962. Per C. Elton). Moss from trees and wall (Pont Hill, Cornwall, Mrs. R. E. Teagle, 24.ii.1957). Litter under yew



FIGS. 198–202. *Pergamasus* (*Paragamasus*) *lapponicus* Trägårdh, female.
Fig. 198 dorsum of idiosoma. Fig. 199 venter. Fig. 200 tectum. Fig. 201 chelicera.
Fig. 202 trochanter of leg IV.

(summit of Box Hill, Surrey, A. H. G. Alston, 15.i.1956). Hornbeam humus (Bookham Common, Surrey, Mrs. R. E. Teagle, xi.1956). Holly humus (near Groombridge, Sussex, P. N. Lawrence, 3.iii.1957). In oak and beech leaf mould (Grasmere, Westmorland, J. T. Salmon, 26.vi.1951). Heath and birch (St. Faith's Common, Horsford, Norwich, Norfolk, J. T. Salmon, 13.v.1951). In leaf mould (Leith Hill, Surrey, J. T. Salmon, 16.vi.1951). In leaf mould (Richmond Park, Surrey, J. T. Salmon, 19.iii.1951). Moss from crevices in rocks (near Force Forge, Westmorland, M. E. Bacchus, 2.xii.1954). In leaf mould (Boltons Wood, Boltons Abbey, North Riding, Yorkshire, J. T. Salmon, 24.v.1951). In leaf mould (Burnham Beeches, Bucks., J. T. Salmon, 3.vi.1951). Oak humus (Gwydyr Forest, North Wales, P. N. Lawrence, 22.x.1961). Moss on boulder (Llandudno, North Wales, P. N. Lawrence, 12.xi.1961). Rhododendron humus (Swansea University, Swansea, P. N. Lawrence, 26.iii.1962). Turf among bracken (Clyne Common, Swansea, P. N. Lawrence, 29.iii.1962). Bracken litter (Bishopston Common, Swansea, S. K. Bhattacharyya, 4.i.1961). Floor of scotch fir wood (Aviemore, Inverness, J. T. Salmon, 7.vii.1951). In moss (Tarbet, Crianlarich, Loch Lomond, Dunbarton, J. T. Salmon, 3.vii.1951).

Pergamasus (Paragamasus) leruthi Cooreman

Pergamasus leruthi Cooreman, J. (1951). *Bull Mus. Hist. nat. Belge.* **27**, 42 : 5, figs.

MALE. The dorsal shield (732μ long × 382μ wide) is without a median transverse suture and yellow in colour. The distribution of setae on the dorsal shield is shown in Text-fig. 203.

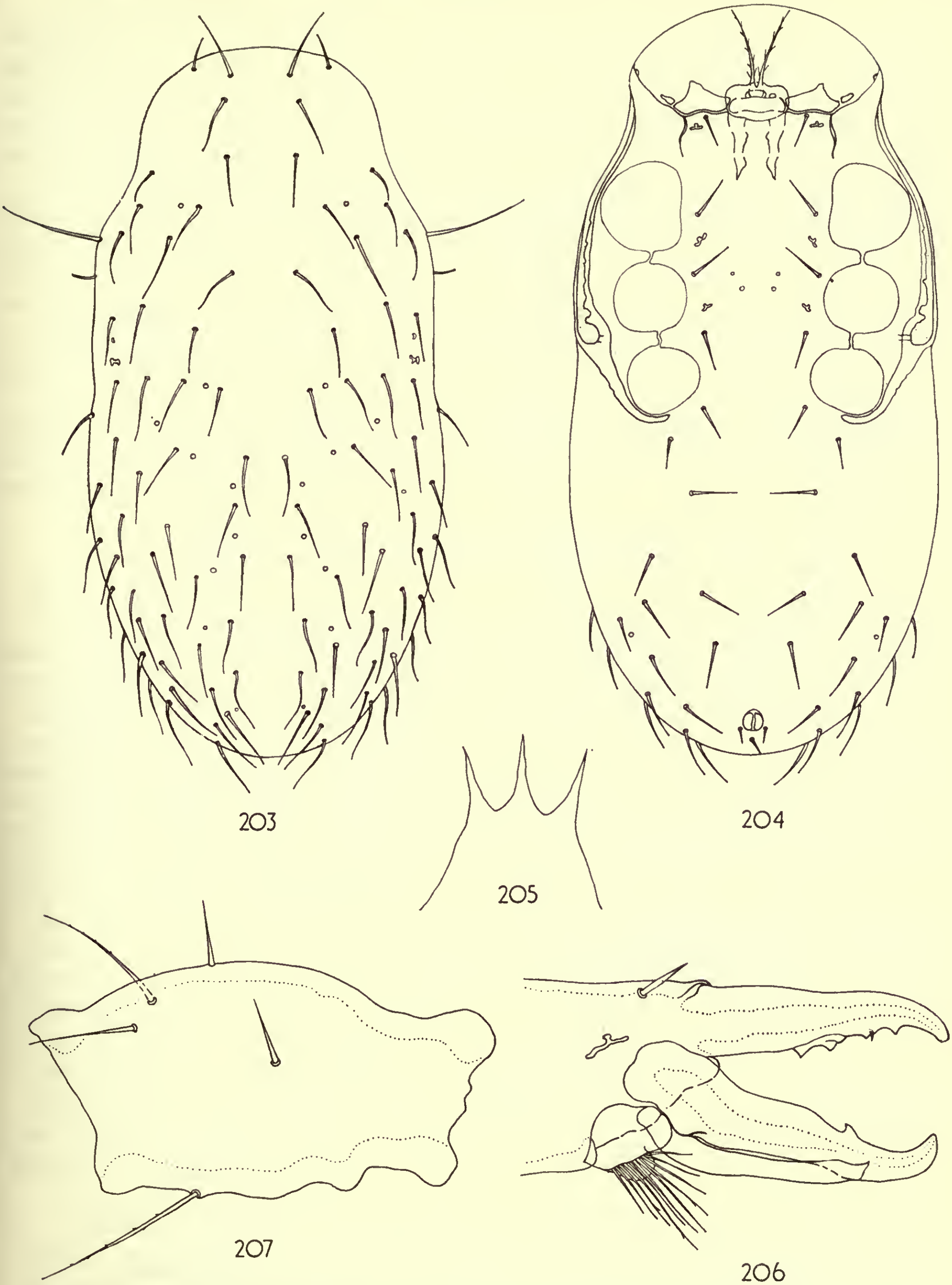
The tritosternum is provided with a pair of pilose laciniae. The distribution of the prae-endopodal shields is shown in Text-fig. 204. The genital lamina is not produced into a median spine. There is a pair of undulating fissures which extend downward from the anterior margin of the sternal shield (Text-fig. 204). The stigma is situated between coxae III and IV ; and the peritreme extends to coxa I. The post-stigmatal extension of the peritrematal shield reaches coxa IV.

The tectum is three-pronged (Text-fig. 205). The palpal trochanter is without a prominence ; the femur and genu are provided with a comb-like and two spatulate setae, respectively. The terminal end of the fixed digit is slightly blunt and provided with a simple seta ; the movable digit is unidentate, with a spermadactyl process (Text-fig. 206). The corniculus is stalked.

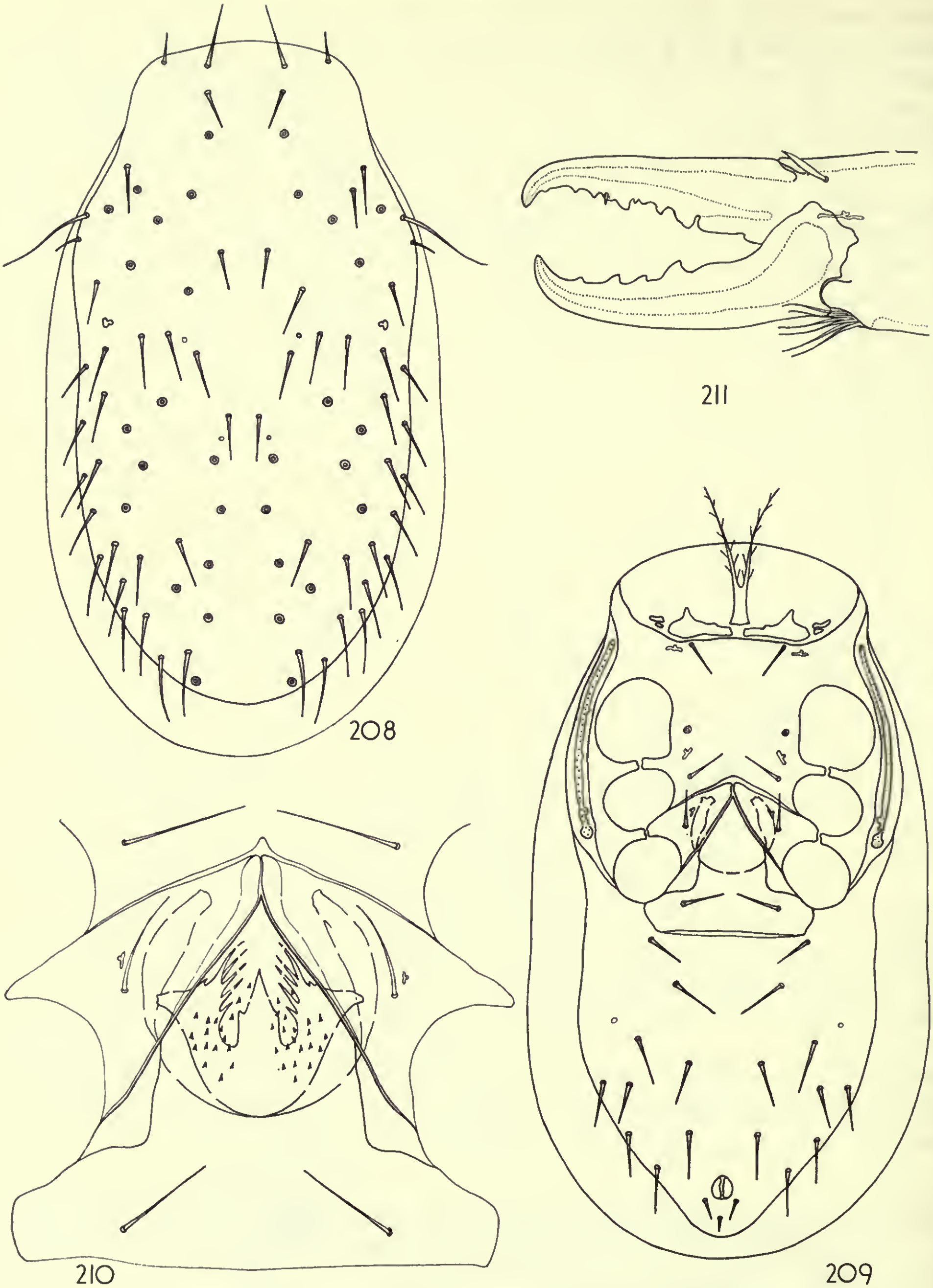
The tibia, tarsus and prae-tarsus of leg I are 126–166μ, 187–208μ and 17–21μ long, respectively. Leg II (Plate 4e) is remarkable for the peculiar shape of the spurs present on the genu and tibia. The trochanter of leg IV is as shown in Text-fig. 207.

FEMALE. The dorsal shield (882μ long × 457μ wide) is sclerotized. The distribution and relative lengths of the dorsal setae are shown in Text-fig. 208.

The tritosternum has an elongated basal part and a pair of pilose laciniae. The distribution of the prae-endopodal shields is shown in Text-fig. 209. The metasternal shields are free. The endogynium has a pair of horns. The endogynial process is very complicated (Text-fig. 210). The opisthogastral shield bears only



Figs. 203–207. *Pergamasus* (*Paragamasus*) *leruthi* Cooreman, male.
Fig. 203 dorsum of idiosoma. Fig. 204 venter. Fig. 205 tectum. Fig. 206 chelicera.
Fig. 207 trochanter of leg IV.



Figs. 208–211. *Pergamasus* (*Paragamasus*) *leruthi* Cooreman, female.
Fig. 208 dorsum of idiosoma. Fig. 209 venter. Fig. 210 magnified structure of the sterniti-genital region. Fig. 211 chelicera,

nine pairs of setae (excepting three setae associated with the anus). The stigma is situated between coxae III and IV ; and the extension of the peritreme is not clearly distinguishable from the damaged specimen. The entire peritrematal shield is coalesced with the ventral shield. The post-stigmatal extension of the peritrematal shield reaches to coxa IV.

The tectum is three-pronged. The pedipalp is similar to that of the male. The fixed digit of the chelicera is furnished with a row of closely-set teeth ; the movable digit is with four teeth (Text-fig. 211).

The tibia, tarsus and prae-tarsus of leg I are 158–166µ, 225–229µ and 21µ long, respectively.

DISTRIBUTION AND HABITAT. This species has been recorded from Roumania (Cooreman, 1951).

I have found only one male from Scotland, in dead leaves (Loch Lomond, between Glasgow and Tarbet, Dunbarton, J. T. Salmon, 8.vii.1951). I have examined Cooreman's specimens of both sexes. The above description and figures of the female are based on the paratype.

Pergamasus (Paragamasus) londonensis sp. nov.

MALE. Unknown.

FEMALE. The dorsal shield (474–483µ long × 267–283µ wide) is light yellow in colour and not heavily sclerotized. The anterior half of the dorsal shield bears twenty-one pairs of setae and the posterior half about twenty pairs (Text-fig. 212).

Ventrally, the tritosternum has a long basal part and a pair of pilose laciniae. The distribution of the prae-endopodal shields in relation to the tritosternum is shown in Text-fig. 213. The metasternal shields are free. The endogynial structure is comparatively simple. The genital shield is shown in Plate 7j. The opisthogastral shield is provided with only eight pairs of setae (excepting the three setae associated with the anus). The stigma is situated between coxa III and IV ; and the peritreme extends to coxa I.

The tectum is three-pronged (Text-fig. 214). The trochanter, femur and genu of the pedipalp are similar to those in *P. rothamstedensis*. The chelicera is shown in Text-fig. 215. The hypostomal processes and deutosternal denticles resemble those of the female of *P. rothamstedensis*.

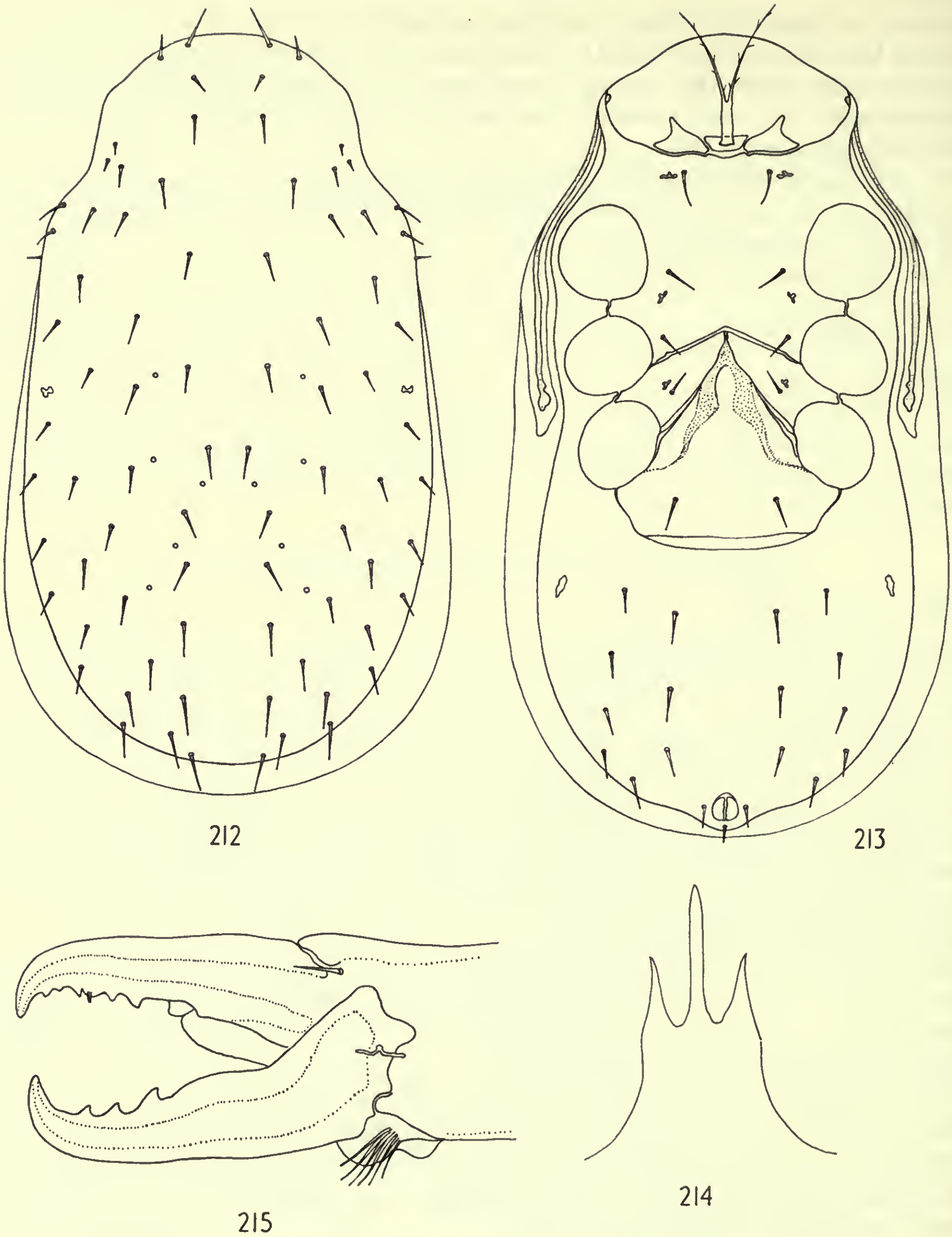
The tibia, tarsus and prae-tarsus of leg I are 70µ, 116–121µ and 8–12µ long, respectively. The trochanter of leg IV is devoid of prominences.

HABITAT. I have examined four females from *Salix* sp. litter (British Museum (Nat. Hist.), London, S. K. Bhattacharyya, 5.iii.1962) and have designated a female as the Holotype (1963.2.7.11).

Pergamasus (Paragamasus) longisetosus sp. nov.

MALE. Unknown.

FEMALE. The dorsal shield (974–1,000µ long × 632µ wide) is reddish-brown in colour and strongly sclerotized. The dorsal setae are comparatively long (some of

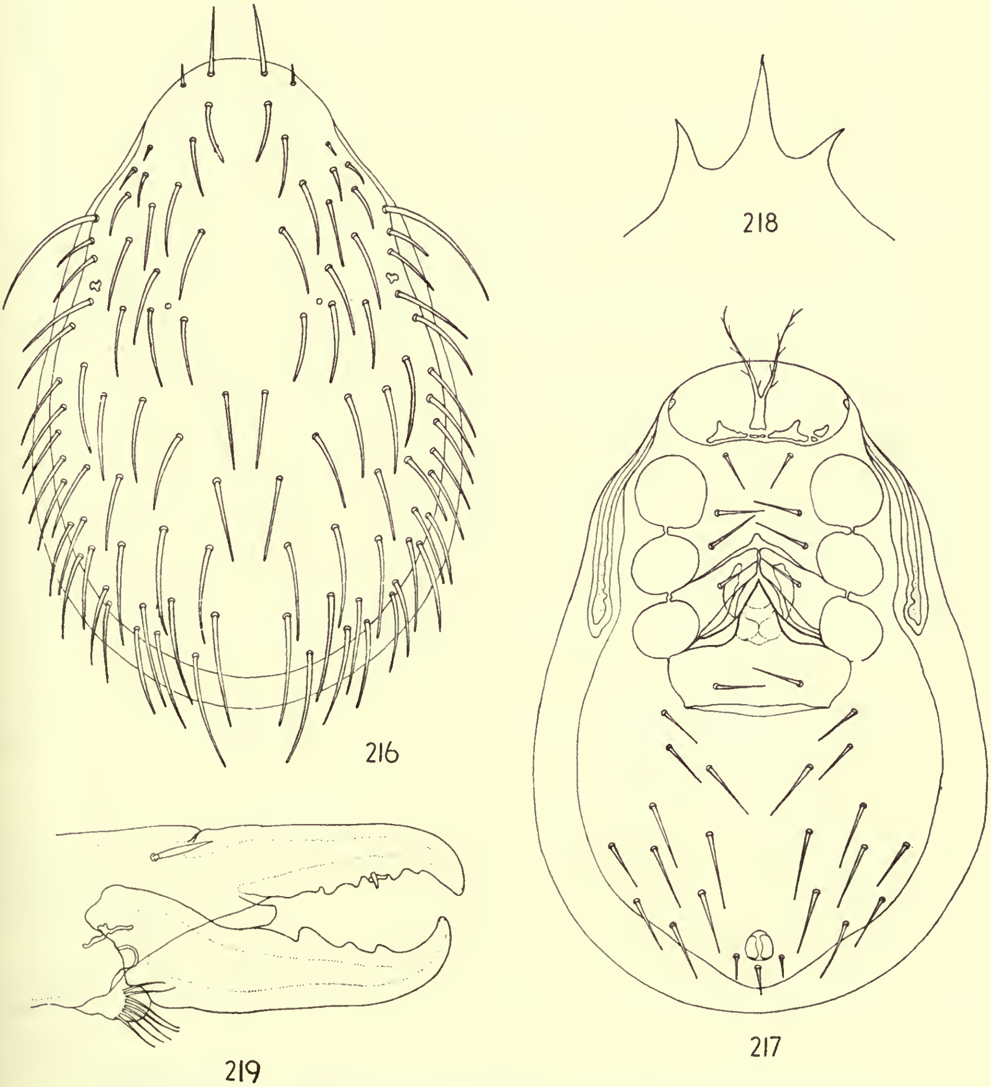


FIGS. 212–215. *Pergamasus* (*Paragamasus*) *londonensis* sp. nov., female. Fig. 212 dorsum of idiosoma. Fig. 213 venter. Fig. 214 tectum. Fig. 215 chelicera.

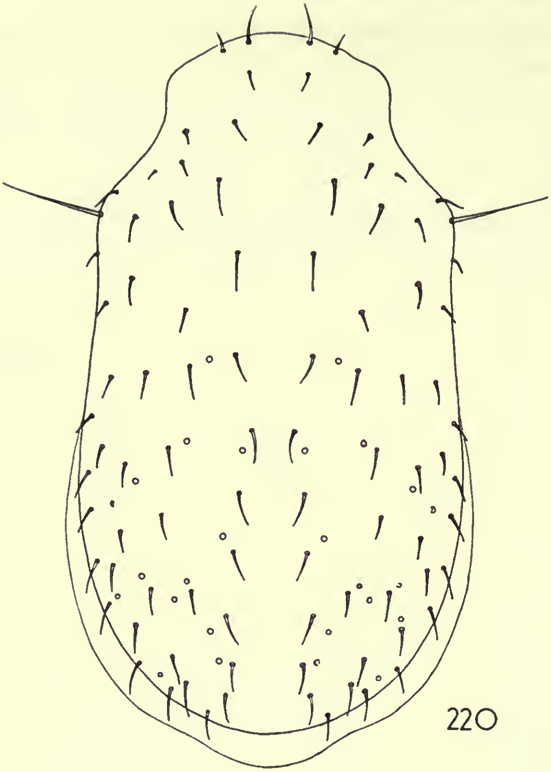
them sparsely ciliated) and stout, and their distribution is shown in Text-fig. 216. The podonotal shield has an invariable number of setae (twenty-one pairs) but the number of setae on the opisthonotal shield is about twenty-eight pairs.

Ventrally, the tritosternum has a pair of pilose laciniae. The prae-endopodal shields are present. The posterior margin of the sternal shield has a short median incision. The metasternal shields are free. The endogynium has a pair of horns and its process is comparatively simple. The setation of the opisthogastral shield is shown in Text-fig. 217. The stigma is situated between coxae III and IV ; the peritreme extends to the level of coxa I.

The tectum is three-pronged, the median tine being longer than the lateral ones (Text-fig. 218). The most distinctive features of the chaetotaxy of the pedipalp



Figs. 216–219. *Pergamasus* (*Paragamasus*) *longisetosus* sp. nov., female. Fig. 216 dorsum of idiosoma. Fig. 217 venter. Fig. 218 tectum. Fig. 219 chelicera.



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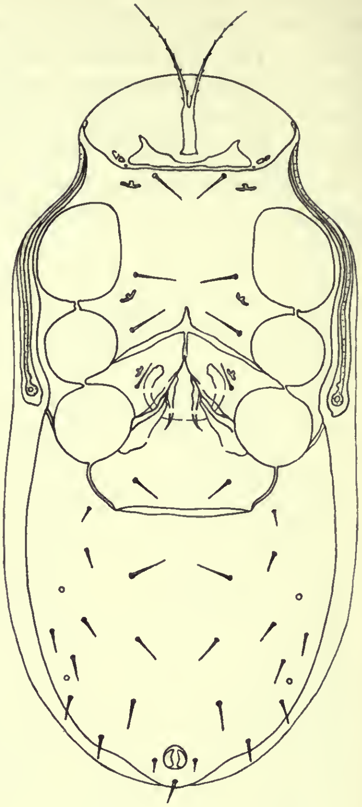

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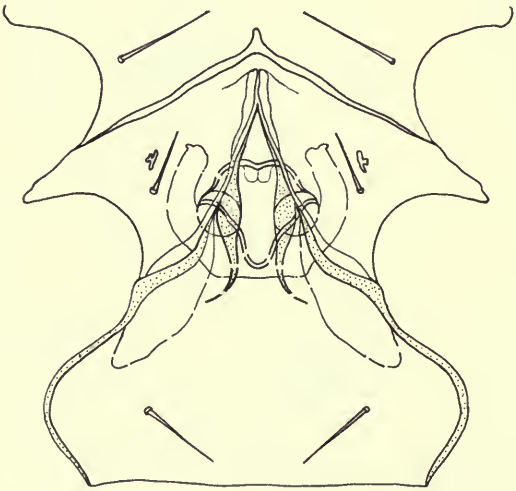

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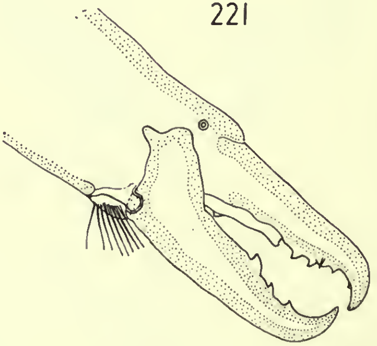

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FIGS. 220–223. *Pergamasus* (*Paragamasus*) *minimus* sp. nov., female.
Fig. 220 dorsum of idiosoma. Fig. 221 venter. Fig. 222 magnified structure of the sterniti-genital region. Fig. 223 chelicera.

are ; the comb-like seta on the femur and the two spatulate setae on the genu. The dentition of the chelicera is shown in Text-fig. 219.

The deutosternal denticles are arranged in ten transverse rows.

The tibia, tarsus and prae-tarsus of leg I are 149–154μ, 204–225μ and 18μ long respectively. The trochanter of leg IV is without any prominence.

HABITAT. One female has been obtained from inside the bark of a fallen elm tree (Harefield, Middlesex, A. H. G. Alston, 22.i.1956), and a single female from the Royal Botanic Gardens, Kew, Surrey, by John L. Gilbert (5.iii.1961).

I have designated the female from Harefield, Middlesex as the Holotype (1963.2.7.8).

Pergamasus (Paragamasus) minimus sp. nov.

MALE. Unknown.

FEMALE. The dorsal shield (500μ long × 265μ wide) is very weakly sclerotized. The dorsal setae are comparatively short (Text-fig. 220).

The tritosternum has an elongated base and a pair of well-developed pilose laciniae. The distribution of the prae-endopodal shields is delineated in Text-fig. 221. The metasternal shields are free. The endogynium has a pair of horn-like structures (Text-fig. 222). The opisthogastric shield has ten pairs of setae (excepting three setae associated with the anus). The stigma is present, between coxae III and IV ; and the peritreme extends as far as the level of coxa I.

The tectum is three-pronged. The most distinctive features of the pedipalp are ; the femur is with a comb-like and the genu with a spatulate seta, respectively. The dentition of the chelicera is shown in Text-fig. 223. Approximately half of the lateral margins of the hypostomal processes are fringed. The deutosternum of the ventral groove of the gnathosoma has nine (ten?) transverse rows of denticles.

Leg I with the tibia 77μ and tarsus 121μ long, the prae-tarsus is 8μ long. The trochanter of leg IV is tuberculated.

HABITAT. I have examined a single female (Holotype 1963 : 2.7.19) from soil and compost (Tettenhall, Stafford, Dr. D. W. Empson, 4.iii.1959).

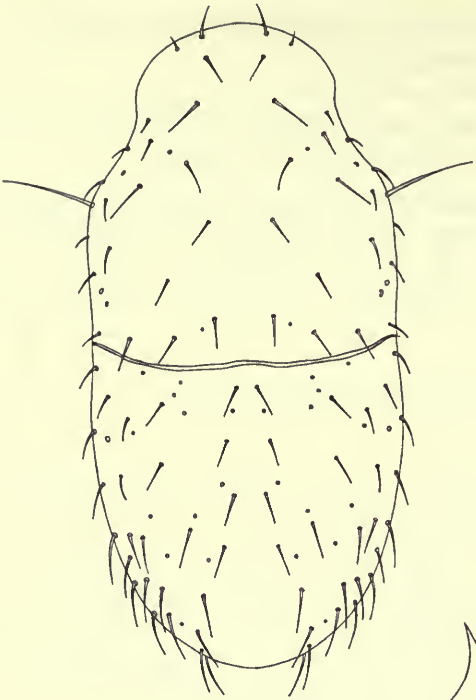
Pergamasus (Paragamasus) misellus Berlese

Gamasus (*Pergamasus*) *misellus* Berlese, A. (1904). *Redia* **1** : 237 ; Berlese, A. (1906). *Redia* **3** : 207, figs.

Pergamasus misellus : Schweizer, J. (1961). *Denks. schweiz. naturf. Ges.* **84** : 49, figs. ; Karg, W. (1962). *Mitt. Zool. Mus. Berlin* **38** : 77, figs.

MALE. The dorsal shield is 515–548μ long and 283μ wide and is provided with a transverse suture (Text-fig. 224). The anterior dorsal shield bears twenty-one pairs of setae.

The tritosternum, prae-endopodal shields and the shape of the genital lamina is shown in Text-fig. 225. The stigma is situated between coxae III and IV ; and the peritreme extends to coxa II. A pair of post-stigmatal setae is present.



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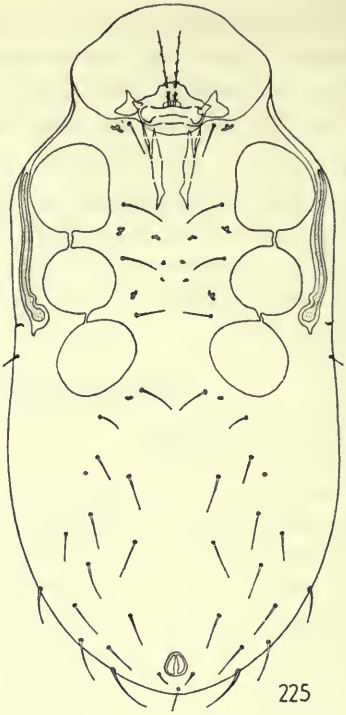

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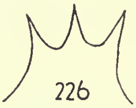

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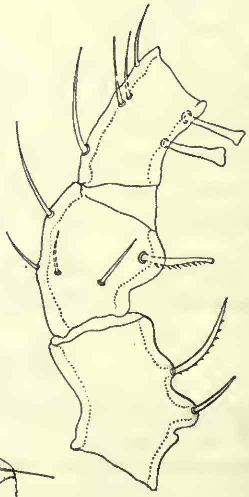

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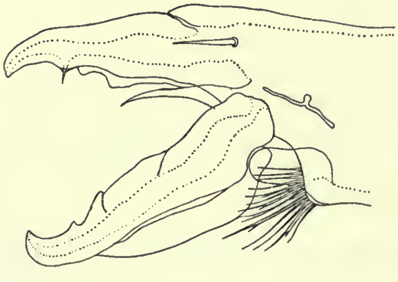

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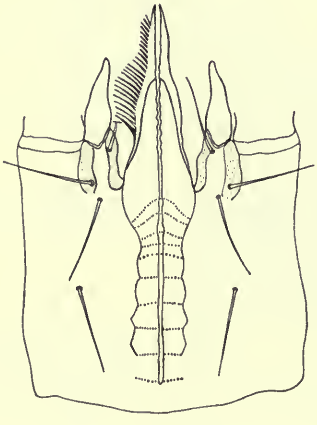

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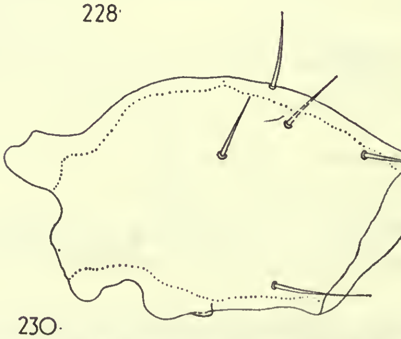

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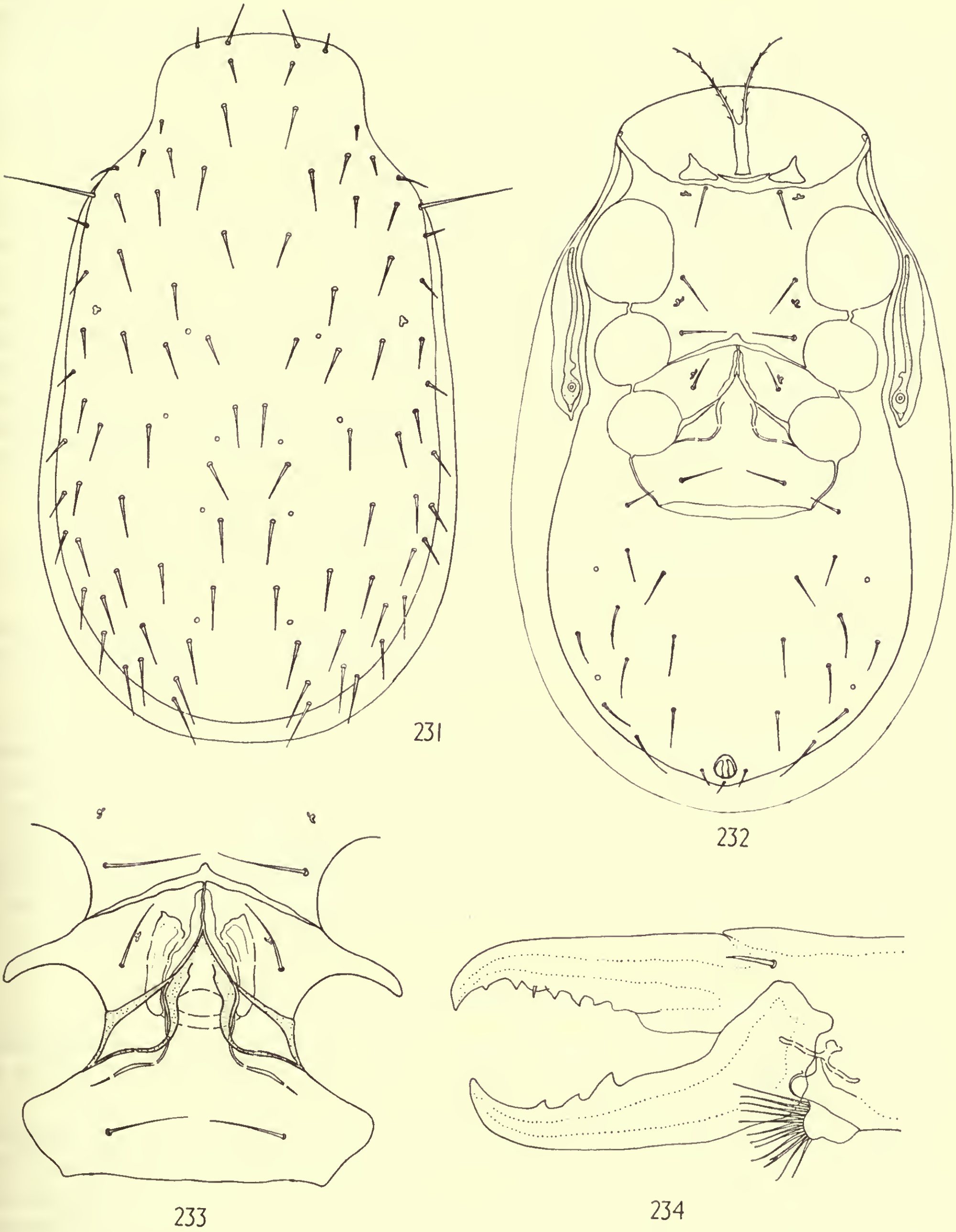
Figs. 224–230. *Pergamasus* (*Paragamasus*) *misellus* Berlese, male.
Fig. 224 dorsum of idiosoma. Fig. 225 venter. Fig. 226 tectum. Fig. 227 trochanter, femur and genu of pedipalp. Fig. 228 chelicera. Fig. 229 venter of gnathosoma. Fig. 230 trochanter of leg IV.



Figs. 231–234. *Pergamasus* (*Paragamasus*) *misellus* Berlese, female.
Fig. 231 dorsum of idiosoma. Fig. 232 venter. Fig. 233 magnified structure of the sterniti-genital region. Fig. 234 chelicera.

The tectum is three-pronged (Text-fig. 226). The distinctive features of the pedipalp are shown in Text-fig. 227. The chelicera is as in Text-fig. 228. The form of the hypostomal processes and rows of deutosternal denticles are shown in Text-fig. 229.

The tarsus of leg I (129–133μ) is longer than the tibia (78–83μ) ; the prae-tarsus being 8μ long. The femur, genu and tibia are spurred (Plate 5a). A tubercle is present on the trochanter of leg IV (Text-fig. 230).

Female. The dorsal shield measures 565–582μ long and 332–339μ wide. The anterior region of the dorsal shield has twenty-one pairs of setae and the posterior region about twenty-five pairs (Text-fig. 231).

Ventrally, the tritosternum has an elongated basal part and a pair of pilose laciniae. The prae-endopodal shields are distributed as in Text-fig. 232. The metasternal shields are free ; and a pair of endogynial horns is present. The enlarged view of the genital region is shown in Text-fig. 233. The genital shield is shown in Plate 8a. There are ten pairs of opisthogastral setae (excepting a pair of paranal and a postanal seta). The position of the stigma and the extension of the peritreme are similar to the male.

The tectum has three prongs. The chelicera is delineated in Text-fig. 234.

The tibia, tarsus and prae-tarsus of leg I are 74μ, 125μ, and 8μ long respectively. The trochanter of leg IV has a tubercle.

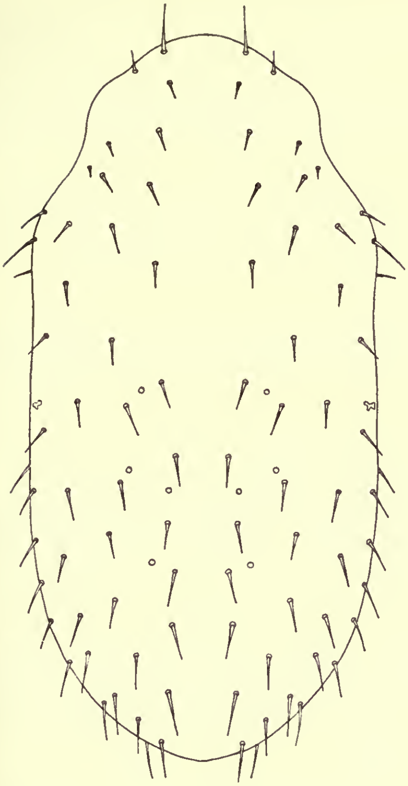
Distribution and habitat. *P. misellus* has been previously recorded from Italy (Berlese, 1904, 1906), Switzerland (Schweizer, 1961) and Germany (Karg, 1962).

I have examined specimens from litter under *Cupressus* sp. (Rothamsted Lodge, Rothamsted Experimental Station, Harpenden, Hertfordshire, G. Owen Evans and E. Browning, 18.iii.1957). *Salix* sp. litter, British Museum (Nat. Hist.), London, S. K. Bhattacharyya, 5.iii.1962). Turf among bracken (Clyne Common, Swansea, P. N. Lawrence, 29.iii.1962). Humus in small wood (Swansea University, P. N. Lawrence, 26.iii.1962). Pine litter (Clyne Park, Swansea, S. K. Bhattacharyya, 4.i.1961). Bracken litter (Bishopston Common, Swansea, S. K. Bhattacharyya, 4.i.1961).

Pergamasus (Paragamasus) nathistmus sp. nov.

Male. The dorsal shield (374μ long × 183μ wide) is weakly sclerotized, regionally reticulated and somewhat oval in shape. The dorsum is devoid of a transverse suture (Text-fig. 235).

Ventrally, there are two large prae-endopodal shields flanking the genital sclerite and partly covered by the genital lamina. The genital lamina has essentially the same shape as in *P. rothamstedensis* sp.n. The basal part of the tritosternum is completely hidden by the genital sclerite. The chaetotaxy of the venter is shown in Text-fig. 236. The stigma is situated between coxae III and IV ; the peritreme extends to coxa I. The post-stigmatal extension of the peritrematal shield is not clearly discernible.



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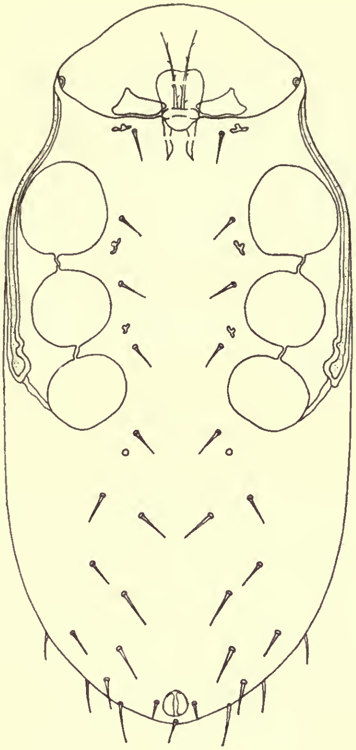

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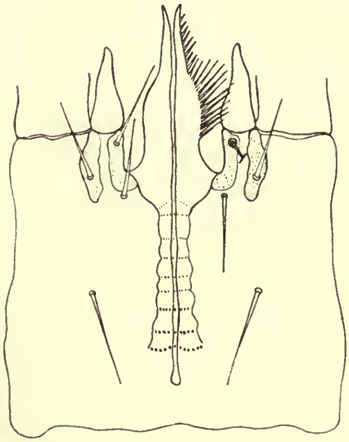

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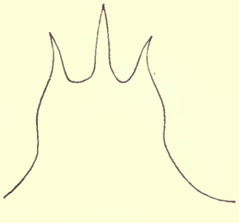

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FIGS. 235–238. *Pergamasus* (*Paragamasus*) *nathistmus* sp. nov., male.
Fig. 235 dorsum of idiosoma. Fig. 236 venter. Fig. 237 tectum. Fig. 238 venter of gnathosoma.

The tectum is three-pronged, the centre prong being longer than the lateral ones (Text-fig. 237). The palp trochanter has no tubercle. The femur has a comb-like seta, and the genu two spatulate setae. Owing to the small size and weakly sclerotized body of the single specimen it did not seem advisable to risk the dissection of the chelicera, so that its dentition is not included in the description. The gnathosoma is shown in Text-fig. 238.

The tibia, tarsus and prae-tarsus of leg I are 60–62µ, 95µ and 8–10µ respectively. Leg II is very weakly spurred (Plate 5b). The femur is not crassate and its main spur is as long as the tibial process.

HABITAT. I have examined a single male (Holotype 1963 : 2.7.9) from *Salix* sp. litter, British Museum (Natural History), London (Coll. S. K. Bhattacharyya, 14.iii.1962).

Pergamasus (Paragamasus) parrunciger sp. nov.

MALE. The dorsal shield (797µ long × 374–382µ wide) is rather weakly sclerotized and provided with a transverse suture (Text-fig. 239). The anterior dorsal shield bears twenty-one pairs of setae and is regionally reticulated. The posterior dorsal shield has about twenty-eight pairs of setae.

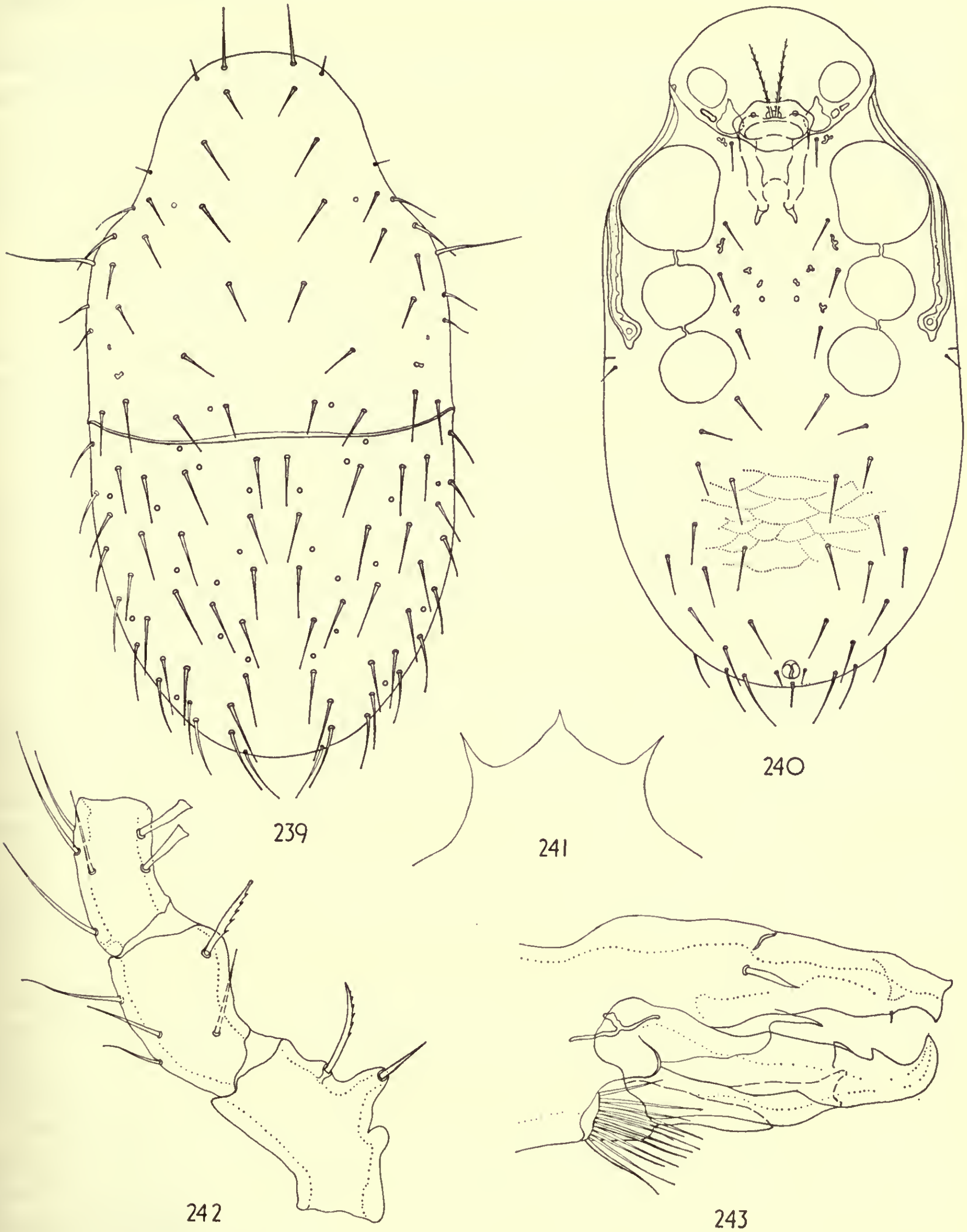
The tritosternal base is extremely reduced and provided with a pair of pilose laciniae. The distribution of the prae-endopodal shields and the shape of the genital lamina is shown in Text-fig. 240. The setation of the opisthogastral shield is as figured. The stigma is situated between coxae III and IV. The peritreme extends to coxa I. A pair of post-stigmatal setae is present.

The tectum is three-pronged (Text-fig. 241). The median tine has a broader base than those of the lateral ones. The trochanter, femur and genu of the pedipalp is shown in Text-fig. 242. The chelicera is robust and its dentition is delineated in Text-fig. 243. Some of the processes of the arthrodial membrane at the base of the movable digit are branched. There is a simple dorsal seta on the fixed digit. The corniculus is distinctly stalked. The lateral margins of the hypostomal processes are fringed.

The tibia, tarsus and prae-tarsus of leg I are 103–128µ, 158–187µ and 14–17µ long respectively. The femur, genu and tibia of leg II are spurred (Plate 5c and e). The femur is crassate. The tibial process may vary in form (Plate 5d). The trochanter of leg IV is simple.

FEMALE. The dorsal shield (747–789µ long × 440–467µ wide) is broadly oval and sclerotized. The anterior half of the dorsal shield bears twenty-one pairs of setae and the posterior half is with twenty-eight. The length of the setae is variable in the posterior half (Text-fig. 244).

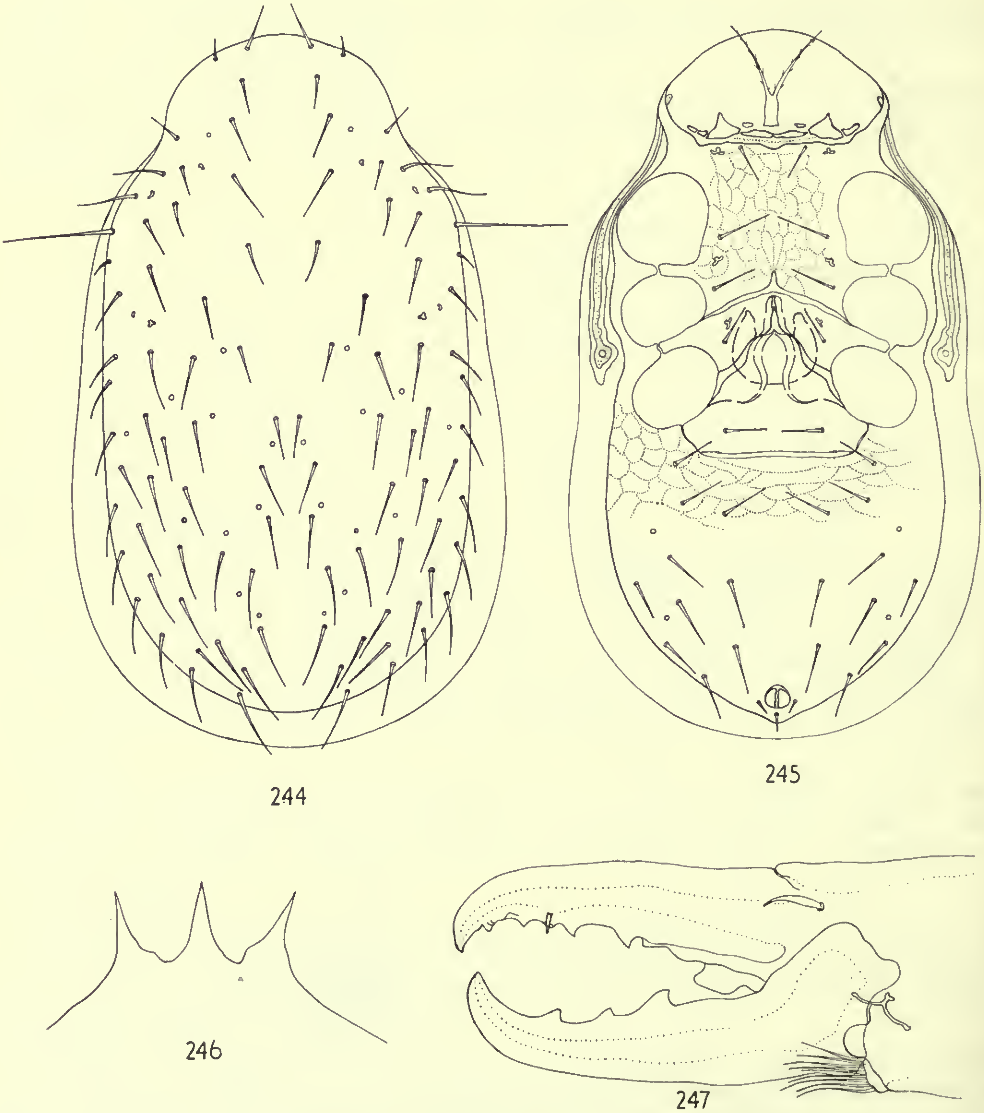
Ventrally, the tritosternum has a pair of pilose laciniae. The distribution of the prae-endopodal shields is shown in Text-fig. 245. The interscutal membrane in between the anterior margin of the sternal and prae-endopodal shields is striated. The endogynium has a pair of horns. The genital shield is shown in Plate 8j. The opisthogastral shield bears ten pairs of setae (excepting three setae associated with



FIGS. 239–243. *Pergamasus* (*Paragamasus*) *parrunciger* sp. nov., male.
Fig. 239 dorsum of idiosoma. Fig. 240 venter. Fig. 241 tectum. Fig. 242 trochanter, femur and genu of pedipalp. Fig. 243 chelicera.

the anus). The stigma is situated between coxae III and IV and the peritreme extends to the level of coxae I. The peritrematal shield extends for a short distance behind the stigma.

The tectum has three prongs of equal length (Text-fig. 246). The palpal femur and genu are with one comb-like and two spatulate setae, respectively. The fixed



Figs. 244–247. *Pergamasus* (*Paragamasus*) *parrunciger* sp. nov., female.
Fig. 244 dorsum of idiosoma. Fig. 245 venter. Fig. 246 tectum. Fig. 247 chelicera.

digit of the chelicera has four well-developed teeth ; the movable finger is tridentate (Text-fig. 247). Approximately the proximal half of the hypostomal processes are fringed.

The tibia, tarsus and prae-tarsus of leg I are 112–129µ, 175–179µ and 12–14µ long respectively. The trochanter of leg IV is without a tubercle.

HABITAT. I have examined five males and nine females from leaf mould (Leith Hill, Surrey, J. T. Salmon, 16.vi.1951) and have designated a male as the Holotype (1963.2.7.19) and a female as the Allotype (1963.2.7.20).

Pergamasus (Paragamasus) rothamstedensis sp. nov.

MALE. The dorsal shield (417µ long × 200–250µ wide) is light yellow in colour and oval in shape. The dorsum is devoid of a transverse suture and the posterior half of the dorsal shield bears a variable number of setae. The setae of the dorsal shield are comparatively short (Text-fig. 248).

Ventrally, the distribution of the prae-endopodal shields is shown in Text-fig. 249. The tritosternum is with a pair of pilose laciniae but its base is completely hidden by the genital sclerite. The anterior margin of the genital lamina is smooth. The distribution of setae on the opisthogastric shield is figured. The stigma is situated between coxae III and IV ; the peritreme anteriorly extends as far as the level of coxa I. Posteriorly the peritrematal shield extends to coxa IV. The post-stigmatal seta is absent.

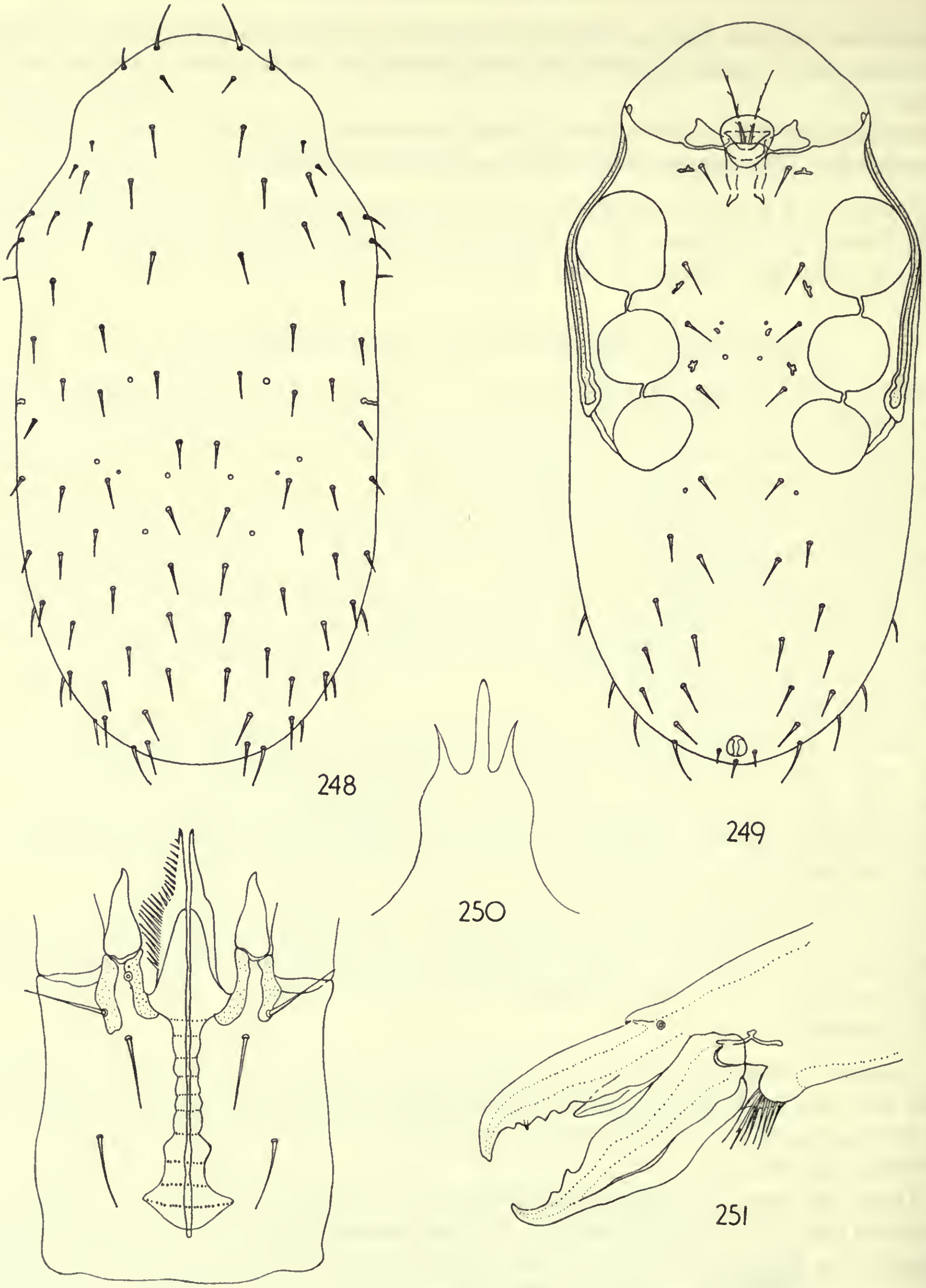
The tectum is three pointed. The median prong is the longest and is blunt (Text-fig. 250). The fixed digit of the chelicera (Text-fig. 251), is tridentate, and the movable digit is bidentate. The palp trochanter is without a tubercle. The corniculus is distinctly stalked (Text-fig. 252). The lateral margins of the hypostomal processes, excepting the basal part, are fringed. The deutosternum has ten transverse rows of denticles.

Leg I has the tibia, tarsus and prae-tarsus 62–66µ, 95–108µ and 8–12µ long, respectively. The femur of leg II (Plate 5f), is with a main and an accessory spur ; and the genual spur is less developed than the tibial process. The trochanter of leg IV is simple.

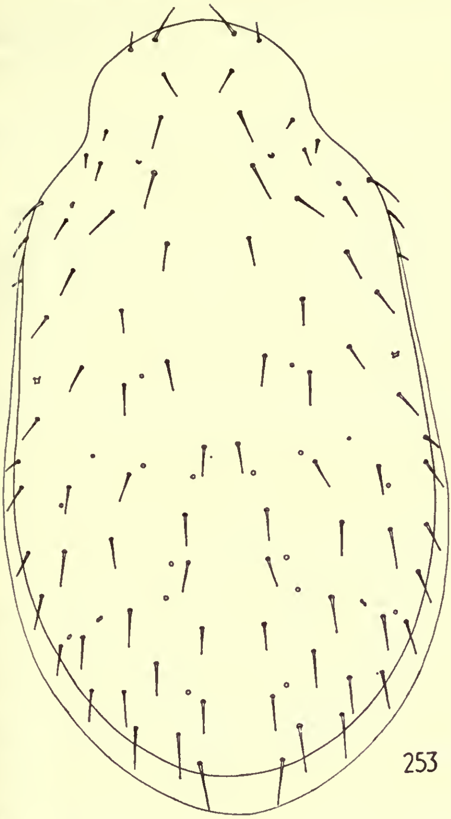
FEMALE. The dorsal shield (450–483µ long × 25–275µ wide) is weakly sclerotized and oval in shape (excepting the anterior region) (Text-fig. 253). The anterior half of the dorsal shield has twenty-one pairs of setae and the posterior half about twenty-two pairs.

There are three prae-endopodal shields, as shown in Text-fig. 254. The tritosternum has a pair of pilose laciniae. The metasternal shields are free. The epigynial shield is as shown in Plate 7k. The opisthogastric shield has eight pairs of setae (excepting the three anal setae). The stigma is situated between coxae III and IV ; and the peritreme extends to coxa I.

The tectum is three-pronged, the median being the longest (Text-fig. 255). The pedipalp is essentially similar to that in the male. The dentition of the chelicera is



FIGS. 248–252. *Pergamasus* (*Paragamasus*) *rothamstedensis* sp. nov., male. Fig. 248 dorsum of idiosoma. Fig. 249 venter. Fig. 250 tectum. Fig. 251 chelicera. Fig. 252 venter of gnathosoma.



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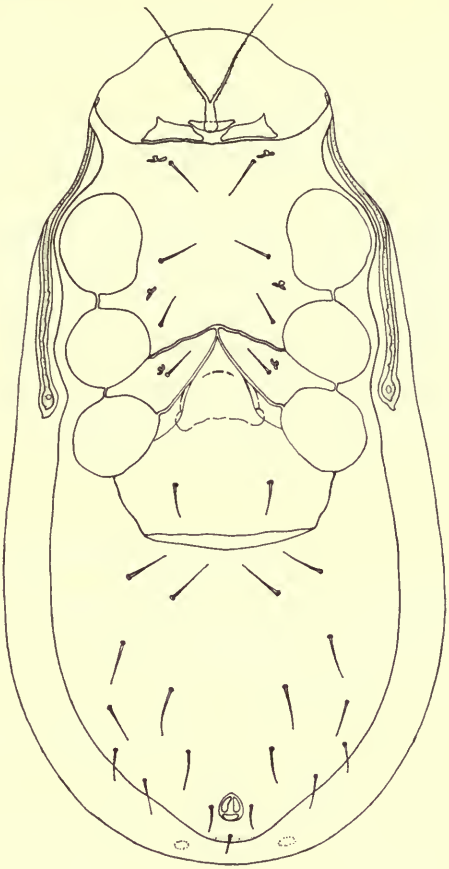

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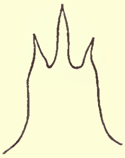

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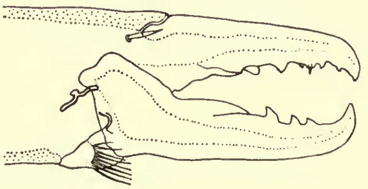

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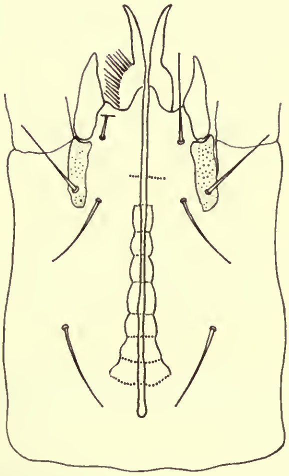

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FIGS. 253–257. *Pergamasus* (*Paragamasus*) *rothamstedensis* sp. nov., female.
Fig. 253 dorsum of idiosoma. Fig. 254 venter. Fig. 255 tectum. Fig. 256 chelicera.
Fig. 257 venter of gnathosoma.

shown in Text-fig. 256. About half of the lateral margins of the hypostomal processes are fringed. The arrangement of the transverse rows of denticles is figured (Text-fig. 257).

The tibia, tarsus and prae-tarsus of leg I are 66–74μ, 106–121μ and 10–12μ long respectively. The trochanter of leg IV is without any tubercle.

HABITAT. I have examined four females from litter under *Cupressus* sp. (Rothamsted Lodge, Rothamsted Experimental Station, Harpenden, Hertfordshire, G. Owen Evans and E. Browning, 18.iii.1957), and two males and four females from *Salix* sp. litter (British Museum (Natural History), London, S. K. Bhattacharyya, 5.iii.1962).

I have designated a male and female from the British Museum (Nat. Hist.), London (Coll. S. K. Bhattacharyya, 5.iii.1962) as the Holotype (1963.2.7.13) and Allotype (1963.2.7.14) respectively.

Pergamasus (Paragamasus) runciger (Berlese)

Parasitus longulus (C. L. Koch) Oudemans, A. C. (1902). *Tijdschr. Ent.* **45** : 37, figs.
Gamasus (*Pergamasus*) *runciger* Berlese, A. (1904). *Redia* **1** : 263 ; Berlese, A. (1906). *Redia* **3** : 214, figs. : Halbert, J. N. (1915). *Proc. R. Irish Acad.* **31** 39 ii : 51, figs.
Pergamasus runciger : Schweizer, J. (1961). *Denks. schweiz. naturf. Ges.* **84** : 54, figs. (in part).

MALE. The dorsal shield (838μ long × 433μ wide) is well sclerotized and provided with a transverse suture. The distribution of the setae on the dorsum is shown in Text-fig. 258.

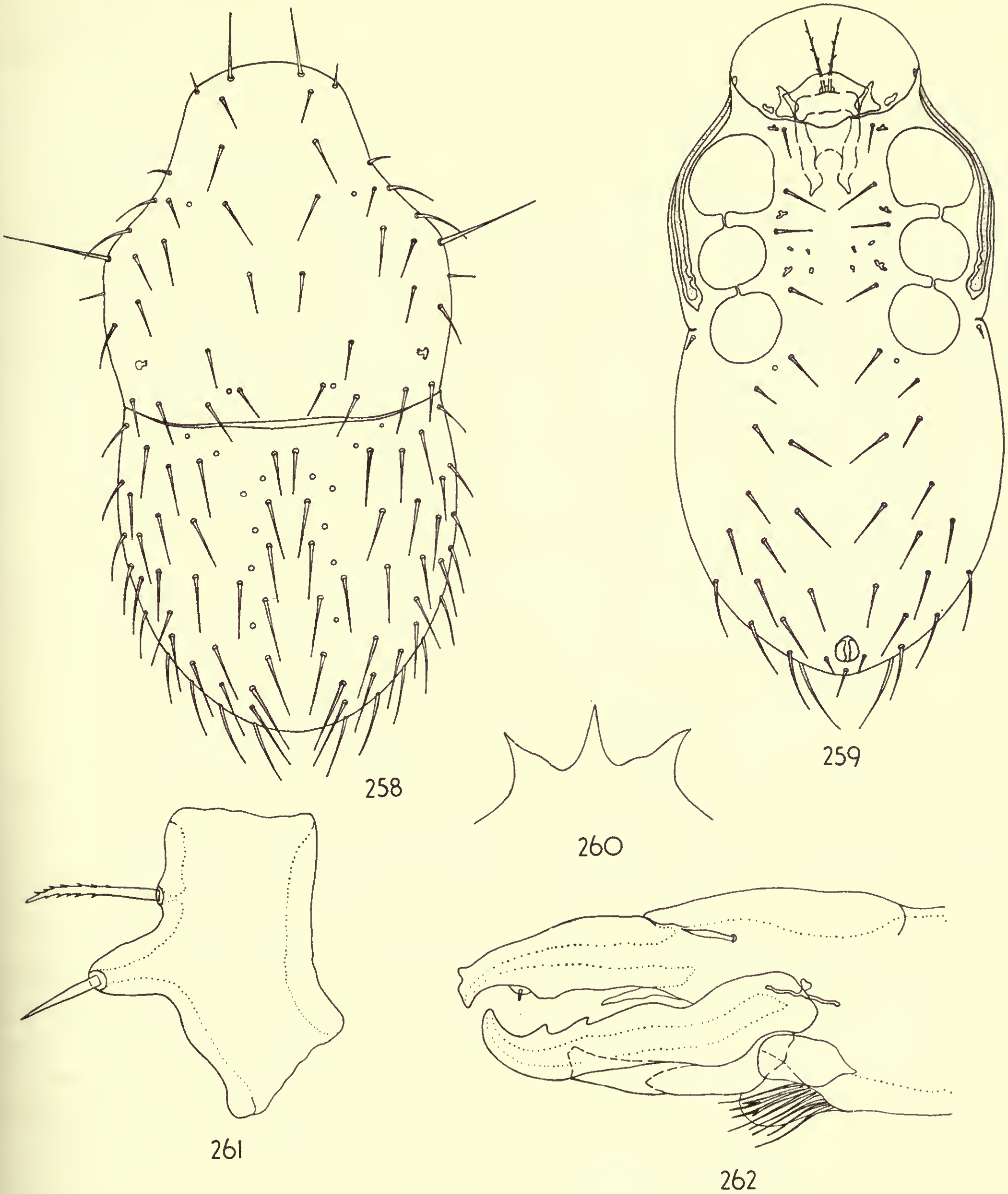
The tritosternum has a pair of pilose laciniae and its base is greatly reduced. The prae-endopodal shield and shape of the genital lamina is shown in Text-fig. 259. The stigma is situated between coxae III and IV ; and the peritreme extends to coxa I. A pair of post-stigmatal setae is present.

The tectum is three-pointed (Text-fig. 260). The distinctive features of the pedipalp are, the trochanter with a seta-bearing tubercle (Text-fig. 261), the femur with a comb-like and the genu with two spatulate setae. The chelicera is shown in Text-fig. 262.

The tibia, tarsus and prae-tarsus of leg I are 112–121μ, 150–154μ and 12μ long, respectively. The femur, genu and tibia of leg II are spurred (Plate 5g and h). The femur is crassate with a main falcate spur and an accessory spur. The trochanter of leg IV is simple.

FEMALE. The dorsal shield (815μ long × 450–483μ wide) is oval (excepting the anteriormost region) and bears about forty-eight pairs of setae of which twenty-one pairs are situated on the podonotal shield (Text-fig. 263).

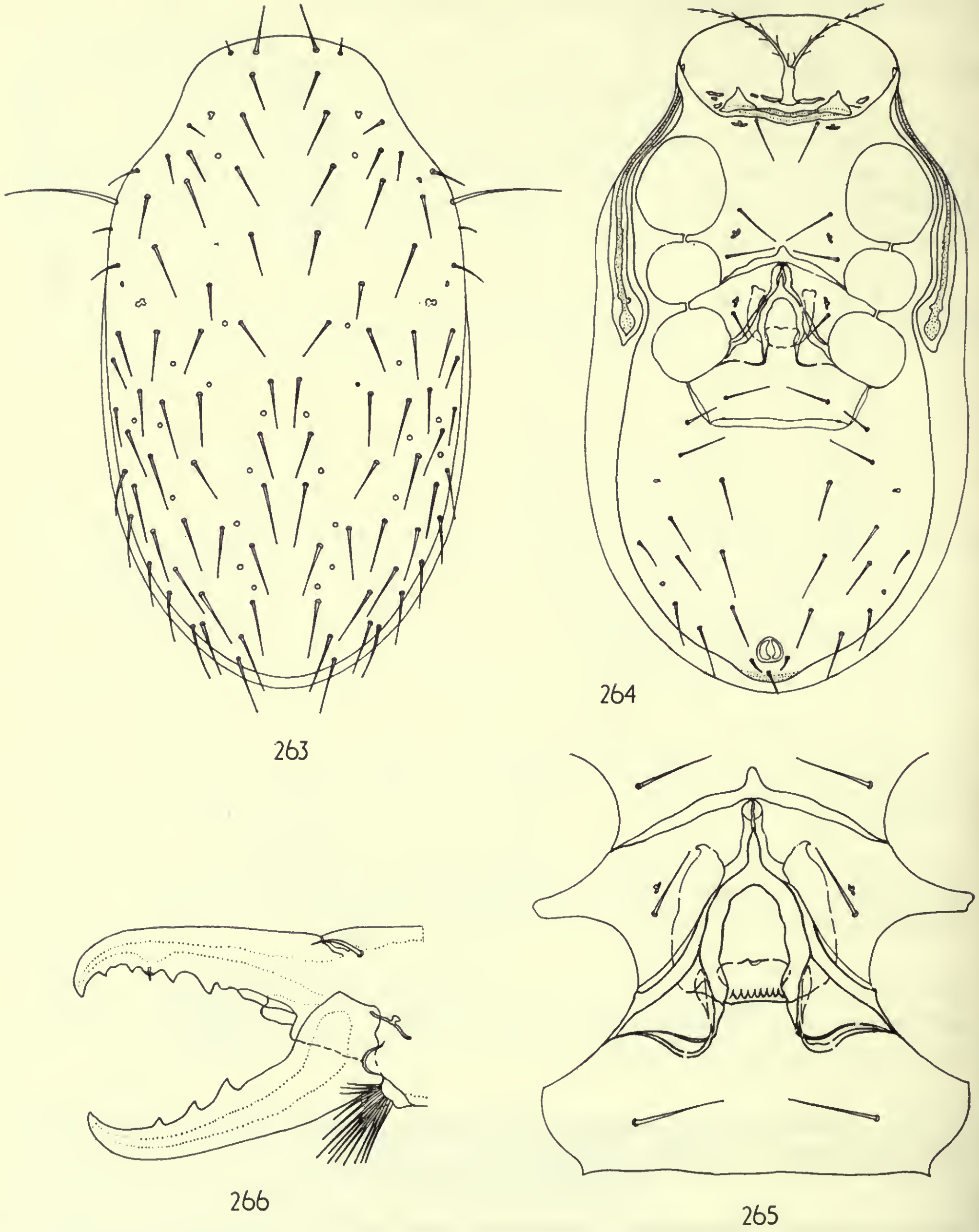
Ventrally, the tritosternum has a well-developed basal part and a pair of pilose laciniae. The distribution of the prae-endopodal shields is shown in Text-fig. 264. The metasternal shields are free. The endogynium has a pair of horns. The epigynial shield and details of the sterniti-genital region are shown in Plate 8k and Text-fig.



FIGS. 258–262. *Pergamasus* (*Paragamasus*) *runciger* (Berlese), male.
Fig. 258 dorsum of idiosoma. Fig. 259 venter. Fig. 260 tectum. Fig. 261 trochanter of pedipalp. Fig. 262 chelicera.

265 respectively. Ten pairs of setae are situated on the opisthogastral shield. The position of the stigma and extension of the peritreme are similar to that in the male.

The tectum is three-pronged. The dentition of the chelicera is shown in Text-fig. 266.



FIGS. 263–266. *Pergamasus* (*Paragamasus*) *runciger* (Berlese), female. Fig. 263 dorsum of idiosoma. Fig. 264 venter. Fig. 265 magnified structure of the sterniti-genital region. Fig. 266 chelicera.

The tibia, tarsus and prae-tarsus of leg I are 121–137μ, 170–191μ and 12–17μ long, respectively. The trochanter of leg IV is without any process.

DISTRIBUTION AND HABITAT. This species has been recorded from Holland (Oudemans, 1902), Norway (Berlese, 1904, 1906), Ireland (Halbert, 1915) and Switzerland (Schweizer, 1961).

I have examined specimens from litter and humus under pines and holly (near Duddleswell, Ashdown Forest, Sussex, K. H. Hyatt, 10.ix.1956). Moss and leaves (Adelaide Hill, Bowness, Cumberland, J. T. Salmon, 29.vi.1951). In marsh debris (Surlingham, Norfolk, J. T. Salmon, 12.v.1951). *Sphagnum*, etc. (Cock Hill, Yorks, J. T. Salmon, 21.vii.1951). In leaf mould (Epping Forest, Essex, J. T. Salmon, 27.v.1951). In litter (Stratton Strawless, near Aylsham, Norwich, Norfolk, J. T. Salmon). Hornbeam humus (Bookham Common, Surrey, Mrs. R. E. Teagle, xi.1956). In oak and beech leaf mould (Grasmere, Westmorland, J. T. Salmon, 26.vi.1951). Algae and rushes (Colletts Bridge, Norfolk, P. N. Lawrence, 16.x.1960). Beech leaf mould (Amersham, Bucks., M. E. Bacchus, 13.v.1951). Moss from crevices in rocks (near Force Forge, Westmorland, M. E. Bacchus, 2.xii.1951). Mosses on rotten wood (Killay, near River Clyne, Hen Parc Wood, Swansea, P. N. Lawrence, 24.iii.1962). Yew and rhododendron humus (26.iii.1962) and moss on tree and humus underneath (Killay, near River Clyne, Swansea, P. N. Lawrence, 24.iii.1962). Pine litter (Clyne Park, Swansea, S. K. Bhattacharyya, 4.i.1961).

Pergamasus (Paragamasus) schweizeri sp. nov.

MALE. The dorsal shield (697μ long × 332–350μ wide) is provided with a transverse suture and tapers posteriorly (Text-fig. 267).

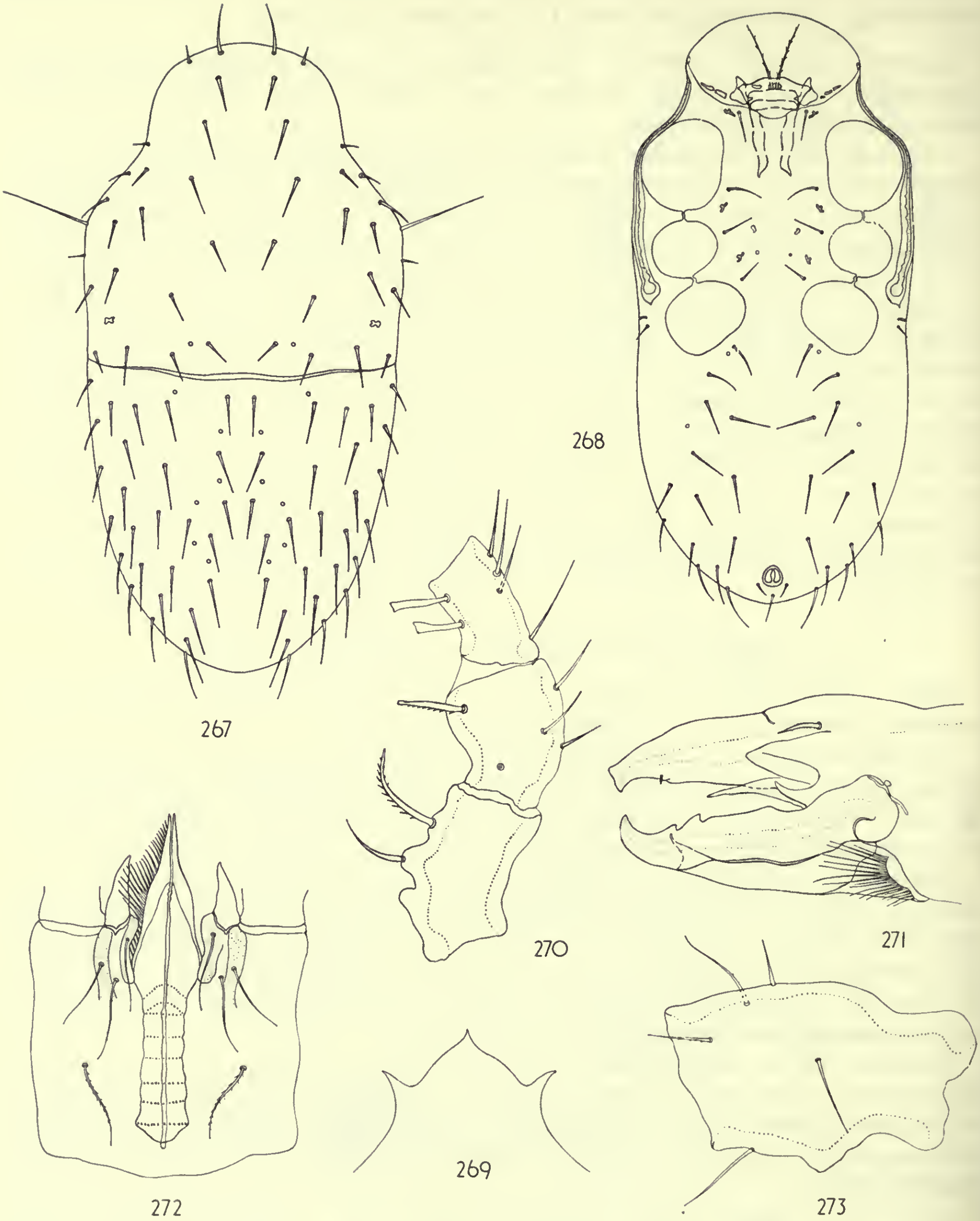
The tritosternal base is completely hidden by the genital lamina. The distribution of the prae-endopodal shields and the shape of the genital lamina is shown in Text-fig. 268. The stigma is situated between coxae III and IV ; and the peritreme anteriorly extends to coxa I. A pair of post-stigmatal setae is present.

The tectum is three-tined (Text-fig. 269). The palp trochanter has two tubercles, and one of them (the distal) bears a simple seta (Text-fig. 270). The palpal femur and genu are provided with one comb-like and two spatulate setae, respectively. The dentition of the chelicera and the form of the spermadactyl process are shown in Text-fig. 271. There are stalked corniculi. The entire lateral margins of the hypostomal processes are fringed (Text-fig. 272).

The tibia, tarsus and prae-tarsus of leg I are 108–121μ, 158–170μ and 12μ long, respectively. The crassate femur of leg II is provided with a strong falcate spur and a small accessory spur ; the genu and tibia are armed (Plate 6a). The distinctive feature of the trochanter of leg IV is constant in all males of the species examined (Text-fig. 273).

FEMALE. The dorsal shield measures 764–797μ long × 367–400μ wide and is provided with about forty-eight pairs of setae (Text-fig. 274).

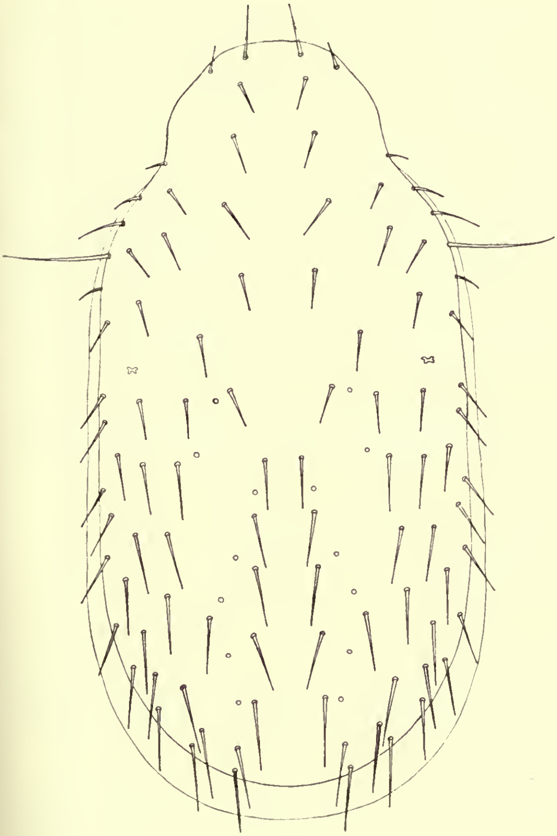
The tritosternum has a pair of pilose laciniae. Ventro-medially, the interscutal membrane between the prae-endopodal shields and the anterior margin of the



FIGS. 267–273. *Pergamasus* (*Paragamasus*) *schweizeri* sp. nov., male. Fig. 267 dorsum of idiosoma. Fig. 268 venter. Fig. 269 tectum. Fig. 270 trochanter, femur and genu of pedipalp. Fig. 271 chelicera. Fig. 272 venter of gnathosoma. Fig. 273 trochanter of leg IV.

sternal shield is striated (Text-fig. 275). The metasternal shields are free. The endogynium has a pair of horns and its process is comparatively simple. The genital shield is shown in Plate 81. The opisthogastral shield is normal, bearing ten pairs of setae. The stigma and peritreme are similar to those in the male.

The tectum is basically three-pronged but shows some variation (Text-fig. 276). The dentition of the chelicera is shown in Text-fig. 277.



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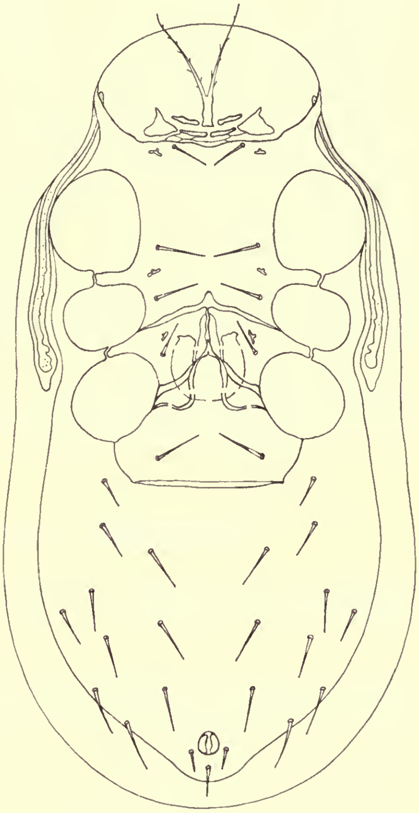

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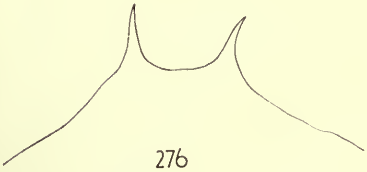

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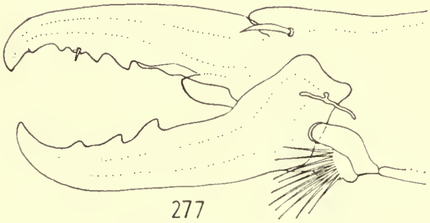

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FIGS. 274–277. *Pergamasus* (*Paragamasus*) *schweizeri* sp. nov., female.
Fig. 274 dorsum of idiosoma. Fig. 275 venter. Fig. 276 tectum. Fig. 277 chelicera.

The tibia, tarsus and prae-tarsus of leg I are 116–129μ, 170–181μ and 12–17μ long, respectively.

HABITAT. I have examined the following material : Seven males and four females from litter under thick evergreen hedge (St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 29.iii.1957). Twenty-two males and twenty females in litter and soil under evergreen trees (St. Agnes, Isles of Scilly, Cornwall, K. H. Hyatt, 5.iv.1957). One male and three females in moss (Grassington, Grass Woods, North Riding, Yorkshire, J. T. Salmon, 24.vi.1951). Two males and two females from moss on tree stumps and stones (Forest of Dean, Gloucestershire, J. T. Salmon, 27.ix.1951). One male from Stratton Strawless (near Aylsham, Norwich, Norfolk, J. T. Salmon, 13.v.195?). Three males and two females from leaf mould (Forest of Dean, Gloucestershire, J. T. Salmon, 27.ix.1951). One male from litter and humus under pines and holly (near Duddleswell, Ashdown Forest, Sussex, K. H. Hyatt, 10.ix.1956). Six males and eight females from lichens in crevices (Moel Siabod, North Wales, P. N. Lawrence, 22.x.1960). One male in mosses on rotten wood (Killay, near River Clyne, Hen Parc Wood, near Swansea, P. N. Lawrence, 24.iii.1962). One male from rotten stump (Gwydyr Forest, North Wales, P. N. Lawrence, 22.x.1960). Two males and two females in moss (Tarbet, Crianlarich, Loch Lomond, Dunbarton, J. T. Salmon, 3.vii.1951).

I have designated a male and a female from St. Agnes, Isles of Scilly (Coll. K. H. Hyatt, 29.iii.1957) as Holotype (1963.2.7.4) and Allotype (1963.2.7.5) respectively.

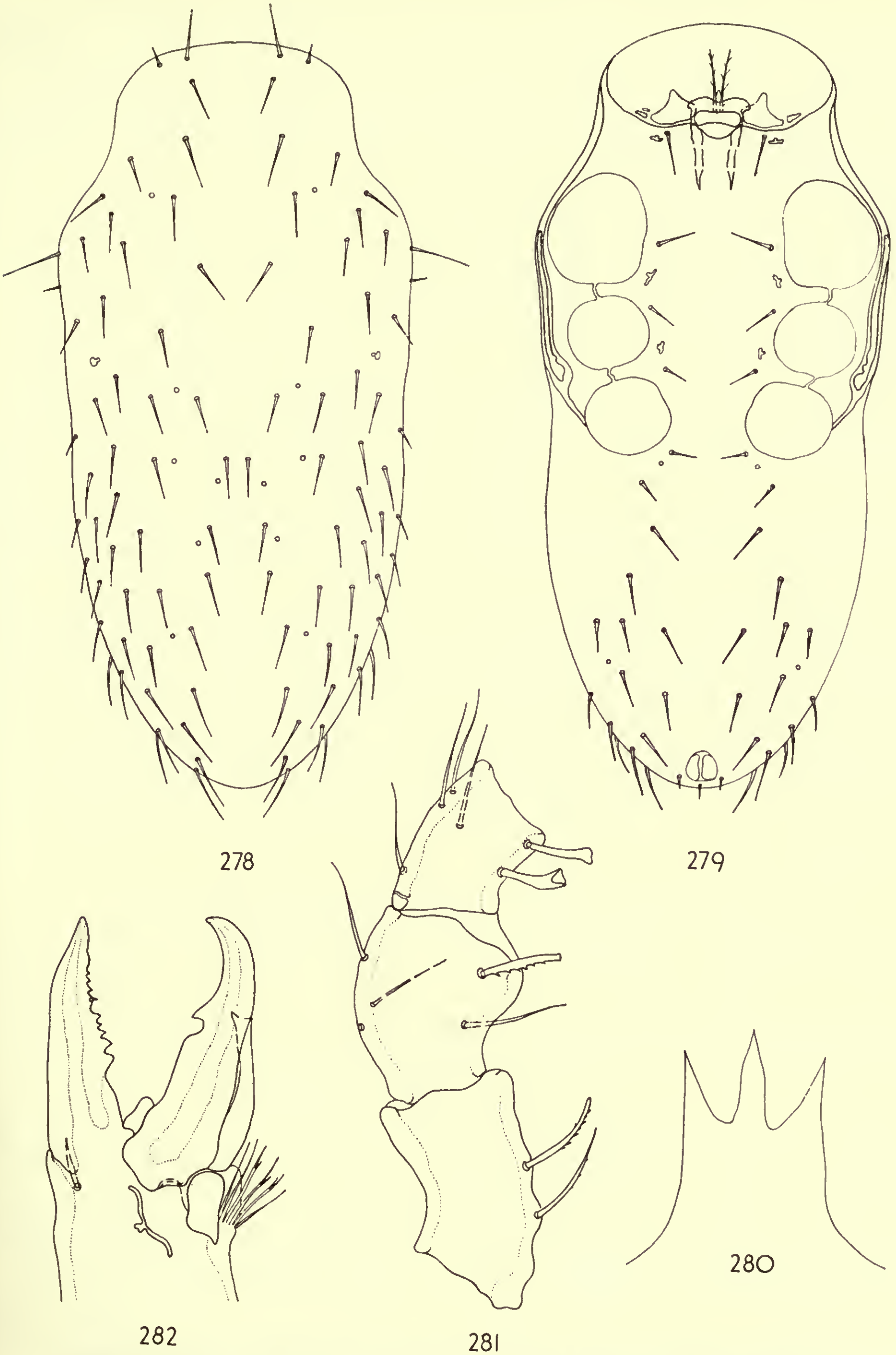
Pergamasus (Paragamasus) suecicus (Trägårdh)

Leptogamasus suecicus Trägårdh, I. (1936). *Ent. Tidskr.* 227, figs. Schweizer, J. (1961). *Denks. schweiz. naturf. Ges.* **84** : 10, figs.

MALE. The dorsal shield (450–467μ long × 240–249μ wide) is deep yellow, well sclerotized and not entirely reticulated. The dorsum is without a median transverse suture and narrows posteriorly (Text-fig. 278).

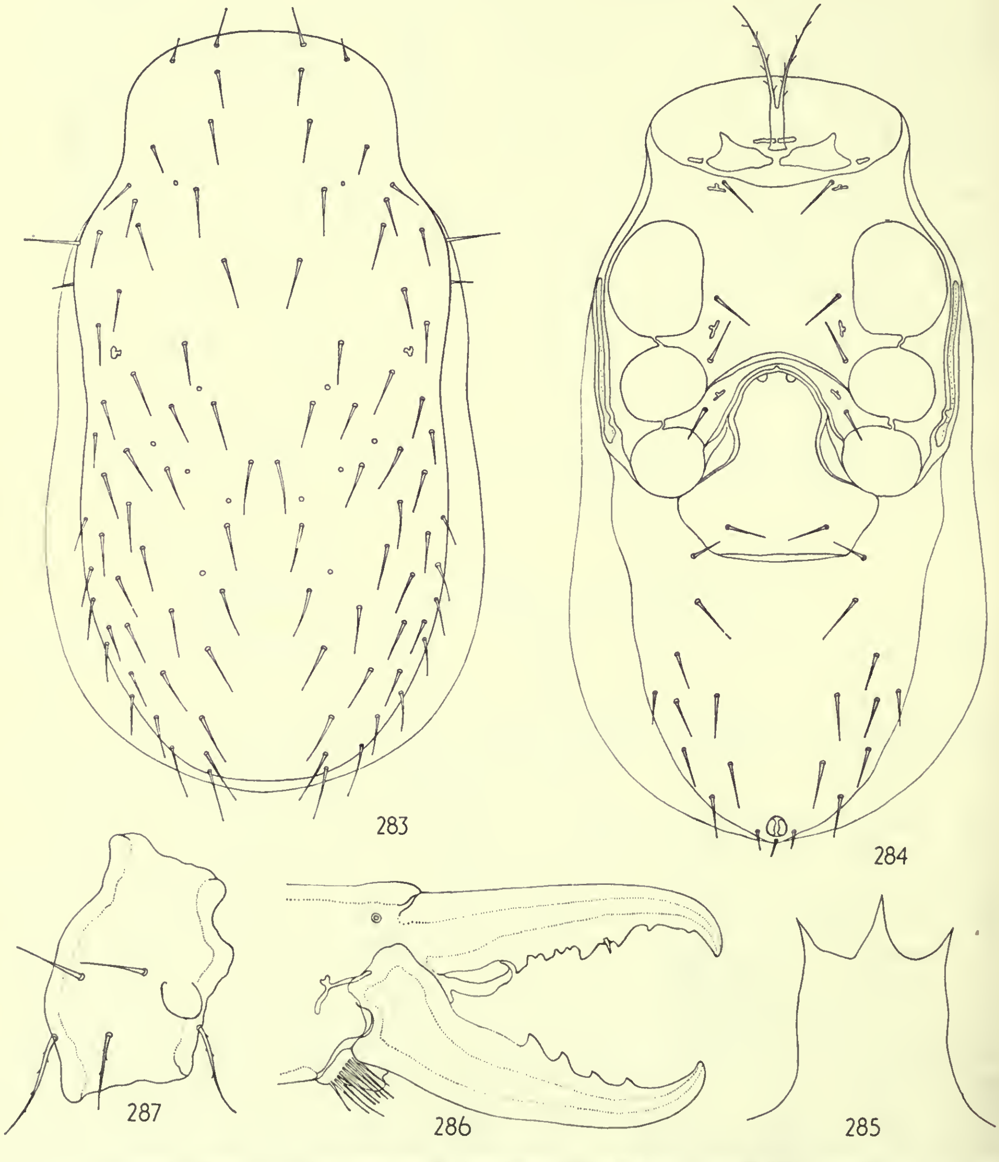
Ventrally, the tritosternum has a pair of well developed pilose laciniae. The basal part of the tritosternum is completely hidden by the genital sclerite. The prae-endopodal shields and pilose laciniae are also partly covered by the genital lamina. The setation of the opisthogastral shield is shown in Text-fig. 279. The stigma is situated between coxae III and IV ; the peritreme reaches to coxa II. The post-stigmatal prolongation of the peritrematal shield extends to coxa IV.

The tectum is three-pronged (Text-fig. 280). The most distinctive features of the pedipalp are, the trochanter without any tubercle, the femur with a comb-like seta and the genu with two spatulate setae (Text-fig. 281). The fixed digit of the chelicera is provided with closely-set teeth of variable size ; a pilus dentilis and a simple dorsal seta are also present (Text-fig. 282). The movable finger is unidentate and the spermadactyl is normal. A number of arthrodial processes, at the base of the movable digit, are branched.



FIGS. 278–282. *Pergamasus* (*Paragamasus*) *suecicus* (Trägårdh), male.
Fig. 278 dorsum of idiosoma. Fig. 279 venter. Fig. 280 tectum. Fig. 281 trochanter, femur and genu of pedipalp. Fig. 282 chelicera.

The tibia, tarsus and prae-tarsus of leg I are 74–78μ, 109–112μ and 8–10μ long, respectively. The femur, genu and tibia of leg II are spurred (Plate 6b). The femur is crassate, with a strong falcate main spur and an accessory spur. The genual spur is smaller than the tibial spur and almost rounded in shape. Trochanter IV is weakly tuberculated.



Figs. 283–287. *Pergamasus* (*Paragamasus*) *suecicus* (Trägårdh), female. Fig. 283 dorsum of idiosoma. Fig. 284 venter. Fig. 285 tectum. Fig. 286 chelicera. Fig. 287 trochanter of leg IV.

Female. The shape and setation of the dorsal shield (474–490μ long × 249–256μ wide) are shown in Text-fig. 283. The dorsal shield bears about forty-seven pairs of setae of which twenty-one pairs are situated on the anterior half. The number of setae is only variable on the posterior half of the dorsal shield.

Ventrally, the tritosternum has an elongated basal part and a pair of pilose laciniae. There are three pairs of prae-endopodal shields, distributed as in Text-fig. 284. The metasternal shields are completely fused. Anteriorly, the epigynial shield is rounded in shape, except the anterior extremity, where the shield terminates in a knob-like structure (Plate 7l). The opisthogastral shield is somewhat reduced and bears nine pairs of setae (excepting three setae associated with the anus). The peritrematal shield is completely coalesced with the opisthogastric shield posteriorly ; the peritreme only reaches to coxa II. The narrow, tubular post-stigmatal prolongation of the peritrematal shield extends to coxa IV.

The tectum is three-pronged (Text-fig. 285). The pedipalp is essentially similar to that in the male. The dentition of the fixed digit of the chelicera is figured, and the movable digit has four teeth (Text-fig. 286).

The tibia, tarsus and prae-tarsus of leg I are 78–83μ, 125μ and 8μ long, respectively. The distinctive feature of trochanter IV is shown in Text-fig. 287.

Distribution and Habitat. This species is previously known from Sweden (Trägårdh, 1936), Britain (Evans, 1957) and Switzerland (Schweizer, 1961).

I have examined specimens from soil (Silwood Park, Berkshire, D. K. Choudhuri, 1958.2.13.12–16). (Corby, Northants, B. N. K. Davis, 1958). Larch litter (Merlewood, Lancashire, D. Macfarlane, v.1955). In moss and humus in hollow tree (Swansea University, Swansea, P. N. Lawrence, 26.iii.1962). Moss on cliff (Gwydyr Forest, North Wales, P. N. Lawrence, 22.x.1960).

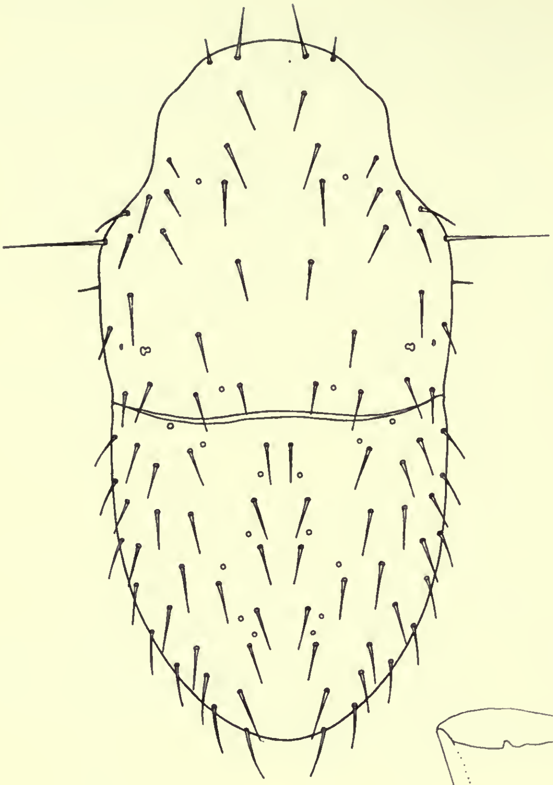
Pergamasus (Paragamasus) teutonicus Willmann

Pergamasus lapponicus Trägårdh var. *teutonica* Willmann, C. (1956). *Československ. parasit.* **33** : 215, figs.

Male. The dorsal shield is 697–732μ long × 350–417μ wide and has a transverse suture. The anterior shield bears twenty-one pairs of setae and the posterior half about twenty-six pairs (Text-fig. 288).

The distribution of the prae-endopodal shields is delineated in Text-fig. 289. The base of the tritosternum and its laciniae are covered by the genital sclerite and lamina. The most distinctive features of the venter are the presence of a rounded setae-bearing scale-like structure near the coxa IV. The setation of the opisthogastric shield is figured. The stigma is situated between coxae III and IV ; and the peritreme reaches to the level of coxa I. A pair of post-stigmatal setae is present.

The tectum is as figured (Text-fig. 290). The palp-trochanter and the dentition of the chelicera are shown in Text-figs. 291 and 292, respectively. The corniculus is stalked.



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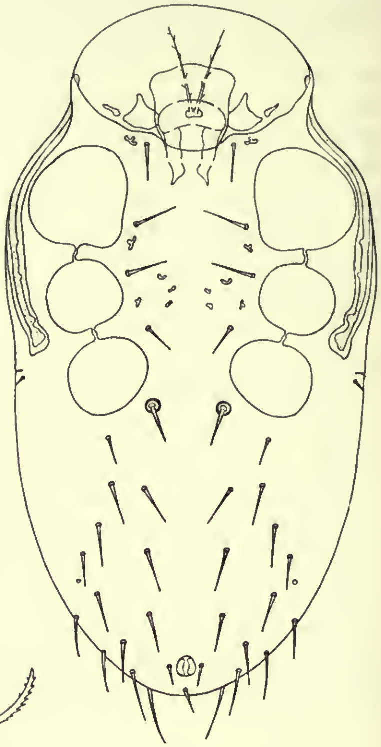

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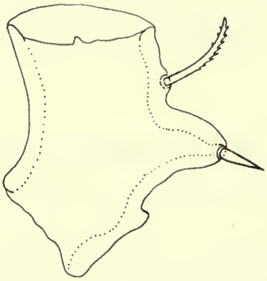

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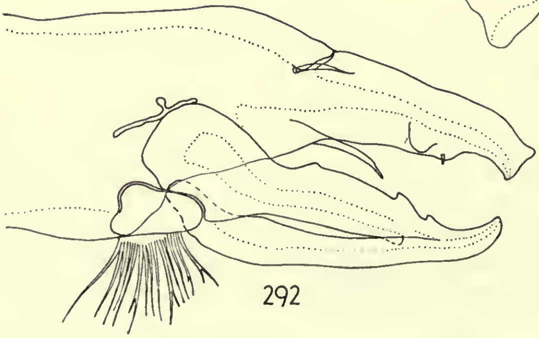

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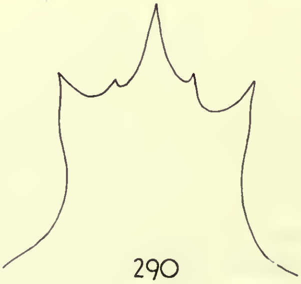

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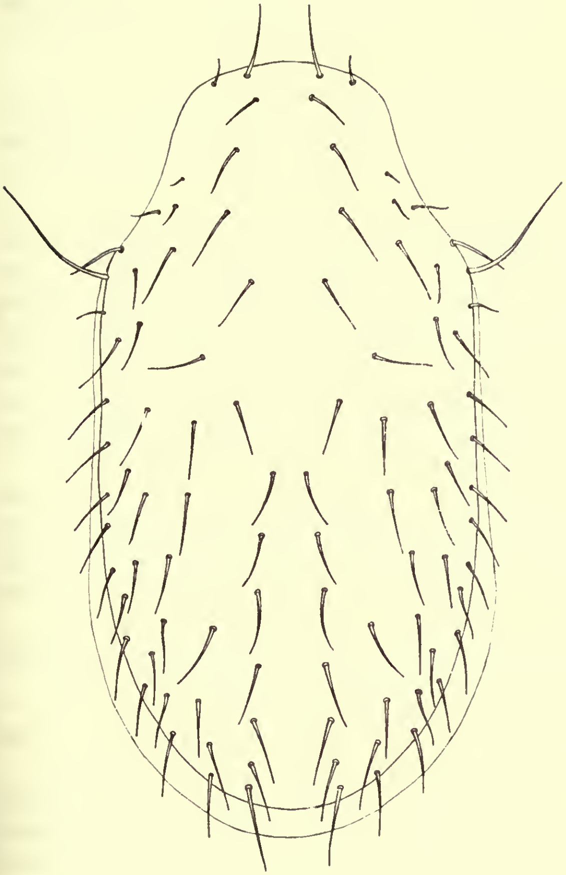
FIGS. 288–292. *Pergamasus* (*Paragamasus*) *teutonicus* Willmann, male.
Fig. 288 dorsum of idiosoma. Fig. 289 venter. Fig. 290 tectum. Fig. 291 trochanter of pedipalp. Fig. 292 chelicera.



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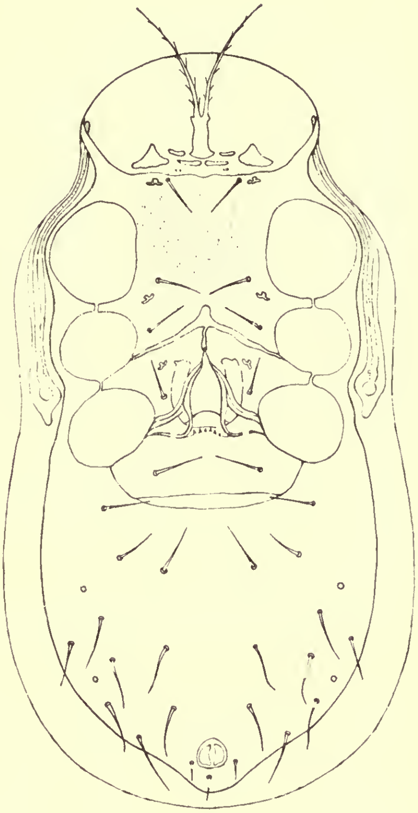

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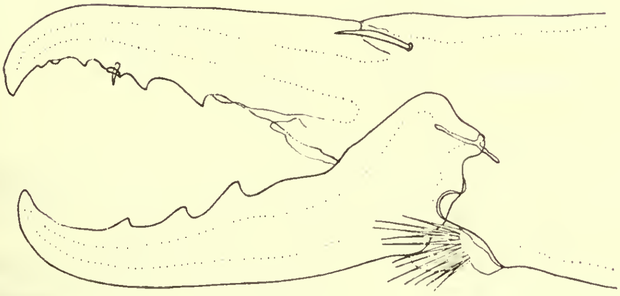

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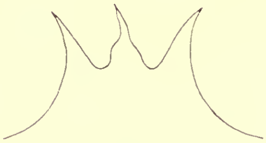

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FIGS. 293–296. *Pergamasus* (*Paragamasus*) *teutonicus* Willmann, female. Fig. 293 dorsum of idiosoma. Fig. 294 venter. Fig. 295 tectum. Fig. 296 chelicera.

The tibia, tarsus and prae-tarsus of leg I are 104–121µ, 164–175µ and 10–17µ long, respectively. The trochanter of leg II is without any tubercle. The femur, genu and tibia are armed with spurs (Plate 6c). The trochanter of leg IV may be with a weakly developed tubercle.

FEMALE. The dorsal shield (697–747µ long × 389–433µ wide) is oval, and yellow in colour and regionally reticulated. The anterior half of the dorsal shield has twenty-one pairs of setae and the posterior half about twenty-seven pairs (Text-fig. 293).

The tritosternum has an elongated base and a pair of pilose laciniae. The distribution of the prae-endopodal shields is shown in Text-fig. 294. The interscutal membrane between the anterior margin of the sternal shield and the prae-endopodal shield is striated. The reticulation of the sternal shield is figured. The metasternal shields are free. The endogynium has a pair of horns. The genital shield is as in Plate 8m and n. The opisthogastral shield, with ten pairs of setae (excepting three setae associated with the anus). The position of the stigma and extension of the peritreme are similar to those in the male.

The tectum is three-pronged (Text-fig. 295). The pedipalp is essentially similar to that of the male except for the absence of the armature on the trochanter. The dentition of the chelicera is as figured (Text-fig. 296). The proximal half of the hypostomal margins are fringed. The deutosternal denticles are arranged in nine to ten transverse rows.

The tibia, tarsus and prae-tarsus of leg I are 104–125µ, 160–183µ and 12–21µ long, respectively. The trochanter of leg IV is without any tubercle.

DISTRIBUTION AND HABITAT. Only the male of this species has previously been recorded from Czechoslovakia (Willmann, 1956).

I have examined material from: under bark of fallen elm tree (Harefield, Middlesex, A. H. G. Alston). Beech leaf mould (Amersham, Buckinghamshire, M. E. Bacchus, 13.v.1951). In beech leaf mould from steep bank (Rickmansworth, Herts., M. E. Bacchus, 25.ii.1951). Soil in aquarium house (Botanic Garden, Cambridge, A. H. G. Alston, 13.iv.1957). In pine litter (Clyne Park, Swansea, S. K. Bhattacharyya, 4.i.1961). Moss and humus in hollow tree (Swansea University, P. N. Lawrence, 26.iii.1962).

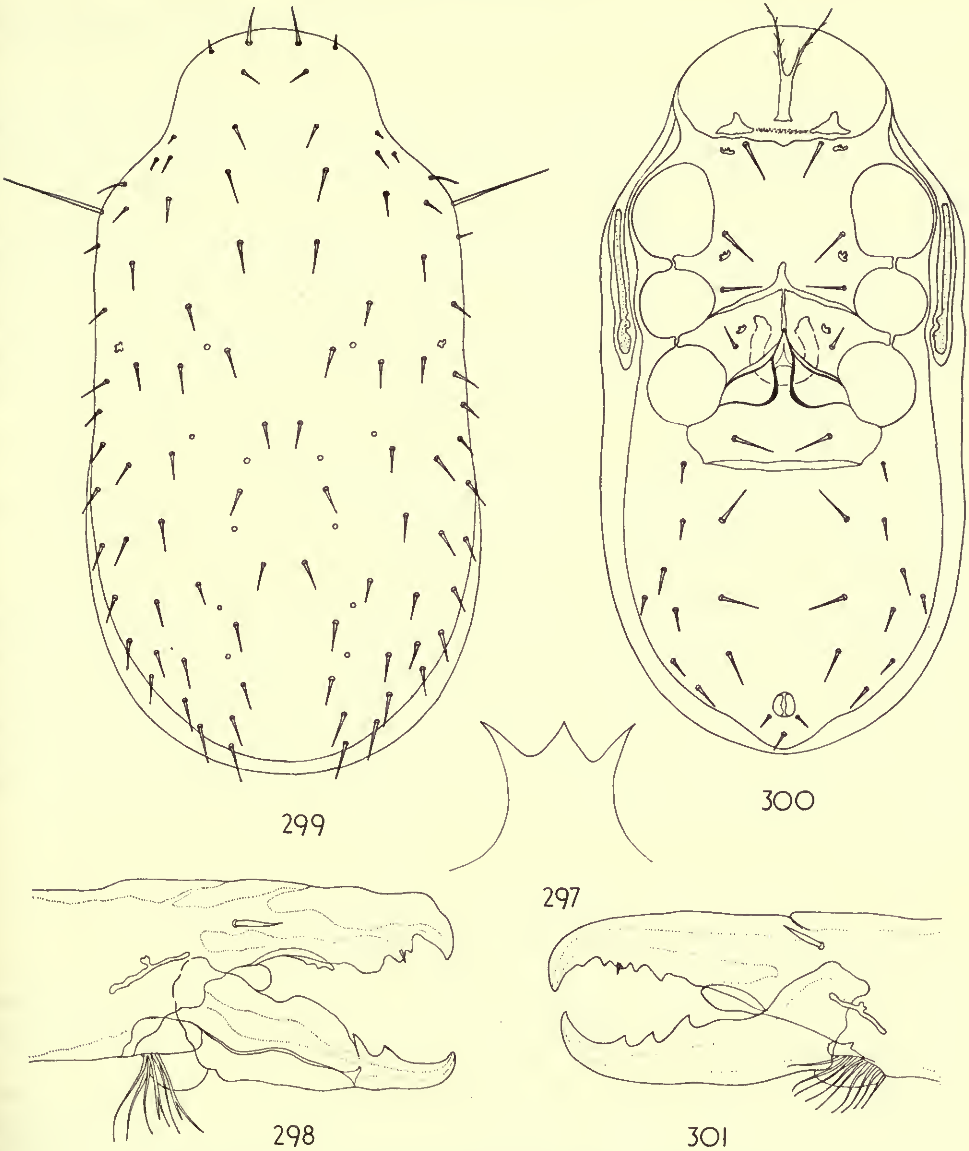
Pergamasus (Paragamasus) truncus Schweizer

Pergamasus truncus Schweizer, J. (1961). *Denks. schweiz. naturf. Ges.* **84** : 44, figs.

MALE. The dorsal shield (515µ long × 240–250µ wide) has a median transverse suture and is lightly sclerotized. The anterior region of the dorsal shield bears twenty-one pairs of setae. The dorsum has comparatively short setae.

The tritosternum has a pair of pilose laciniae. The genital lamina is somewhat similar to that of *P. wasmanni*. The stigma is situated between coxae III and IV; the peritreme extends to coxa II. The post-stigmatal seta is present.

The tectum is three-tined, the median prong being the shortest (Text-fig. 297). The most distinctive features of the pedipalp are: the trochanter is without a



FIGS. 297–301. *Pergamasus* (*Paragamasus*) *truncus* Schweizer.
Fig. 297 tectum of male. Fig. 298 chelicera of male. Fig. 299 dorsum of idiosoma in female. Fig. 300 venter of female. Fig. 301 chelicera of female.

tubercle, the comb-like seta on the femur and the two spatulate setae on the genu are present. The chelicera is shown in Text-fig. 298. The corniculus is distinctly stalked.

The tibia, tarsus and prae-tarsus of leg I are 74–78μ, 108–129μ and 10–12μ long, respectively. The distinctive spurs of leg II are delineated in Plate 6d. The trochanter of leg IV is weakly spurred and the process somewhat resembles that in *P. misellus*.

FEMALE. The dorsal shield (532μ long × 267μ wide) is yellow in colour and provided with comparatively short setae (Text-fig. 299). The anterior region of the dorsal shield bears twenty-one pairs of setae and the posterior region twenty-four pairs.

Ventrally, the tritosternum has an elongated basal part and a pair of pilose laciniae. The distribution of prae-endopodal shields is shown in Text-fig. 300. The endogynium has a pair of horns ; the genital shield is shown in Plate 8b. The opisthogastral shield is with ten pairs of setae (excepting three setae associated with the anus). The stigma is situated between coxae III and IV. Although the peritrematal shield anteriorly extends to the level of coxa I, the peritreme only reaches to coxa II.

The tectum is three-tined. The pedipalp is essentially the same as in the male. The dentition of the chelicera is shown in Text-fig. 301.

The tarsus (116–129μ) of leg I is longer than the tibia (74–80μ). The prae-tarsus is 6–8μ long. The trochanter of leg IV is armed.

DISTRIBUTION AND HABITAT. This species has been recorded only from Switzerland (Schweizer, 1961). I have examined specimens from a number of localities in Wales : Turf among bracken (Clyne Common, Swansea, P. N. Lawrence, 29.iii.1962). Salt marsh debris (Llanrhidian, Glamorgan, P. N. Lawrence, 27.iii.1962). Moorland mosses, *Sphagnum* by stream (S. Llanrhidian, S. Wales, P. N. Lawrence, 27.iii.1962). Mosses on rotten wood (Killay, near River Clyne, Hen Parc Wood, Swansea, P. N. Lawrence, 24.iii.1962). Oak litter (Llew Reservoir, Swansea, S. K. Bhattacharyya, 2.i.1961).

Pergamasus (Paragamasus) wasmanni (Oudemans)

Parasitus wasmanni Oudemans, A. C. (1902). *Tijdschr. Ent.* **45** : 39, figs.

MALE. The dorsal shield (467–483μ long × 240–274μ wide) has a transverse suture (Text-fig. 302). The anterior half of the dorsal shield bears twenty-one pairs of setae.

The tritosternum has a reduced basal part and a pair of pilose laciniae. There is a pair of prae-endopodal shields flanking the genital sclerite. The shape of the genital lamina and the setation of the opisthogastric shield are shown in Text-fig. 303. The stigma is situated between coxae III and IV ; and the peritreme extends to coxa II. A pair of post-stigmatal setae is present.

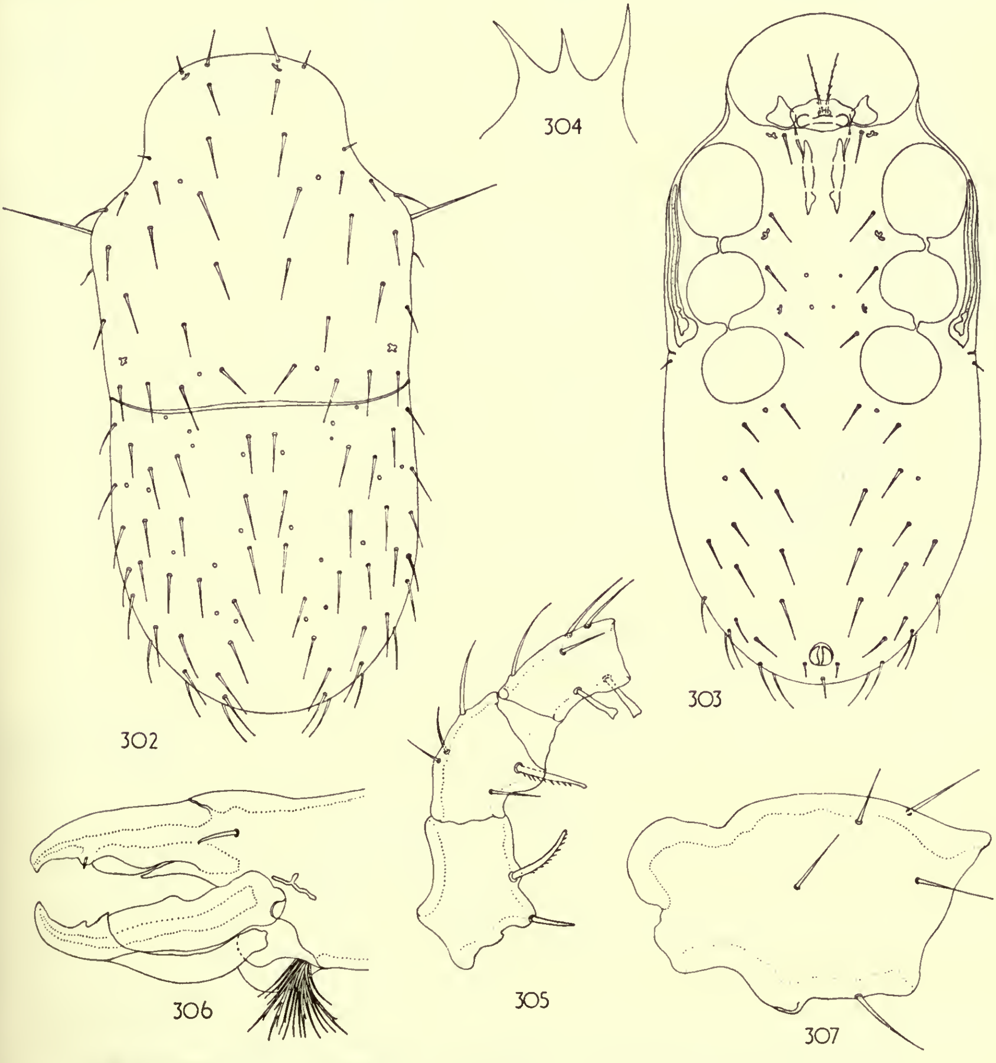
The tectum is three-pronged (Text-fig. 304). The palpal trochanter is tuberculated (Text-fig. 305). The femur and genu are provided with a comb-like and two spatulate setae, respectively. The chelicera is as shown in Text-fig. 305. The spermadactyl is normal. The corniculus is distinctly stalked.

Leg I is with tibia and tarsus 66–78μ and 112–116μ long, respectively ; the prae-tarsus is 10μ long. The diagnostic characters of leg II are shown in Plate 6e.

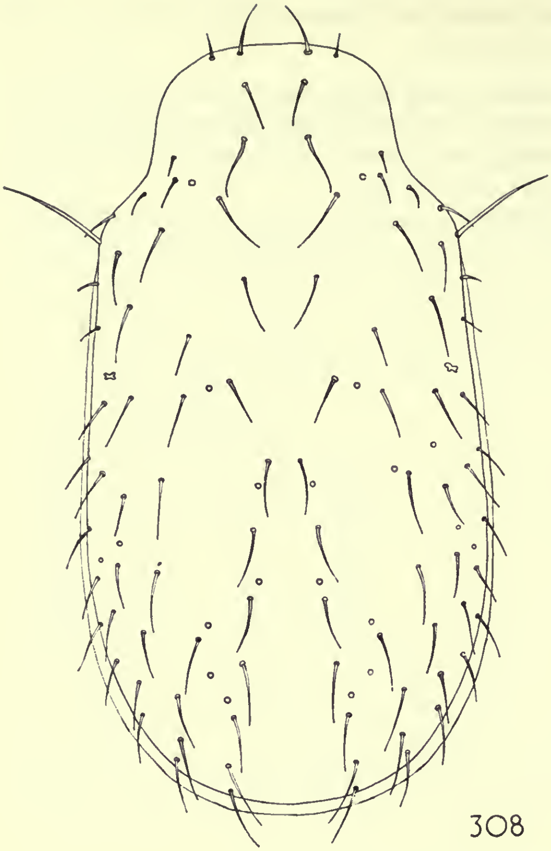
The tibial spur differs from the genual process by being slightly broader. The trochanter of leg IV is delineated in Text-fig. 307.

FEMALE. This sex is weakly sclerotized and light yellow in colour. The dorsal shield (507–522μ long × 267μ wide) is regionally reticulated and provided with about forty-six pairs of setae, of which twenty-one pairs of setae are situated on the anterior half of the dorsal shield (Text-fig. 308).

The tritosternum is biramous. There are three prae-endopodal shields, the median shield being an elongated strip (Text-fig. 309). The interscutal membrane



FIGS. 302–307. *Pergamasus* (*Paragamasus*) *wasmanni* (Oudemans), male.
Fig. 302 dorsum of idiosoma. Fig. 303 venter. Fig. 304 tectum. Fig. 305 trochanter, femur and genu of pedipalp. Fig. 306 chelicera. Fig. 307 trochanter of leg IV.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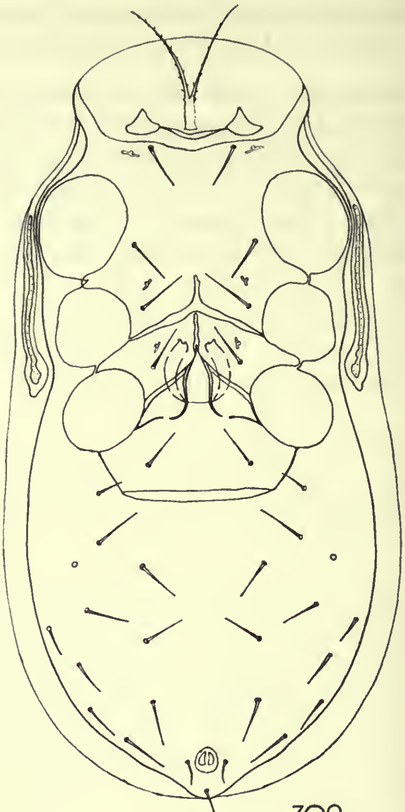
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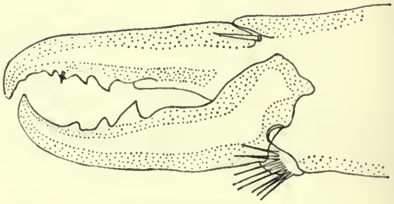
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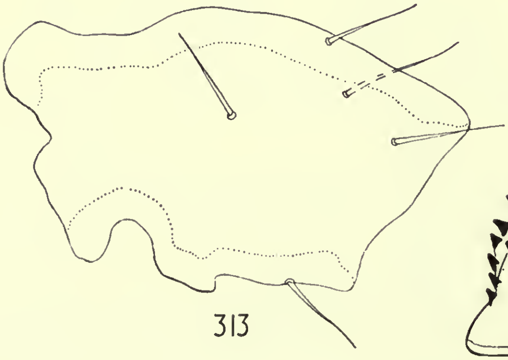
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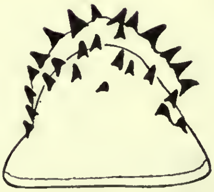
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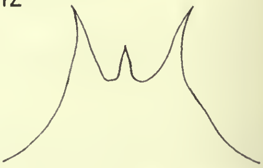
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FIGS. 308–313. *Pergamasus* (*Paragamasus*) *wasmanni* (Oudemans), female. Fig. 308 dorsum of idiosoma. Fig. 309 venter. Fig. 310 endogynial process. Fig. 311 tectum. Fig. 312 chelicera. Fig. 313 trochanter of leg IV.

between the anterior margin of the sternal shield and the prae-endopodal shields is without striations. The metasternal shields are almost fused in the mid-line. The endogynium has a pair of horns and its process is shown in Text-fig. 310. The genital shield is as in Plate 8e. The setation of the opisthogastral shield is figured. The stigma is situated between coxae III and IV. Anteriorly, the peritrematal shield extends to the level of coxa I, but the peritreme reaches to coxa II.

The tectum is three-pointed, the median prong being short and narrow (Text-fig. 311). The pedipalp resembles that of the male but the trochanter lacks tubercles. The chelicera is shown in Text-fig. 312. The lateral margins of the hypostomal processes are fringed. The ventral groove of the gnathosoma is provided with ten transverse rows of deutosternal denticles.

The tibia and tarsus of leg I are 70–74μ and 121–125μ long, respectively ; the prae-tarsus is 8–10μ long. The trochanter of leg IV is tuberculated (Text-fig. 313).

Distribution and habitat. Only the female of this species is previously known from Holland (Oudemans, 1902).

I have examined material from litter and humus under pines and holly (near Duddleswell, Ashdown Forest, Sussex, K. H. Hyatt, 10.ix.1956). Moss and leaves (Adelaide Hill, Bowness, Cumberland, J. T. Salmon, 29.vi.1951). In leaf mould (Savernake Forest, Berkshire, J. T. Salmon, 26.ix.1951). In moss (Grassington, Grass Woods, North Riding of Yorkshire, J. T. Salmon, 24.vi.1951). Leaves from *Sequoia sempervirens* (Virginia Water, Surrey, A. H. G. Alston, 18.xii.1955). (Red Bank, Grasmere, Westmorland, M. E. Bacchus, 3.xii.1954). Oak and rhododendron humus (Penn Ponds, Richmond Park, Surrey, P. N. Lawrence, 10.iii.1957). Holly humus (near Groombridge, Sussex, P. N. Lawrence, 3.iii.1957). Heath and birch (St. Faith's Common, Horsford, Norwich, Norfolk, J. T. Salmon, 13.v.1951). In leaf mould (Burnham Beeches, Buckinghamshire, J. T. Salmon, 3.vi.1951). Rhododendron humus (Swansea University, Swansea, P. N. Lawrence, 26.iii.1962).

RECORDS OF OTHER BRITISH SPECIES OF *Pergamasus* Berlese *s. lat.*

According to " A synonymic Catalogue of British Acari " compiled by Turk (1953) the following species also occur in the British Isles. I have not been able to examine authentic British specimens of these species.

1. *Amblygamasus dentipes* (Koch, 1839).
2. *Pergamasus alpestris* var. *coniger* Hull, 1916.
3. *Pergamasus processiferus* Halbert, 1915.
4. *Pergamasus johnstoni* Oudemans, 1936.
   (nom. nov. pro *Gamasus marginatus* Johnston, 1848 non *Gamasus marginatus* Latr., 1806).
5. *Paragamasus runcatellus* (Berlese, 1906).
   The British records of this species probably refer to *P.* (*Paragamasus*) *schweizeri* sp. nov.
6. *Paragamasus decipiens* (Berlese, 1904).
7. *Paragamasus minor* (Berlese, 1892).

8. *Plesiogamasus paripes* (Hull, 1918).
9. *Plesiogamasus parvulus* (Berlese, 1903).
10. *Plesiogamasus parvulus* var. *dilatatellus* (Berlese, 1906).

The records of *Pergamasus barbarus* Berl. and *Pergamasus mediocris* Berl. given by Turk & Turk (1952) are based on misidentifications ; the species involved being *P.* (*P.*) *septentrionalis* (Oudemans) and *P.* (*P.*) *longicornis* Berlese.

SUMMARY

This work deals with a revision of the British species of the genus *Pergamasus* Berlese s. lat. On the basis of the chaetotaxy of the dorsum of the idiosoma the genus is divided into two subgenera, *Pergamasus* s. str. and *Paragamasus* Hull. Thirty-two species are described, figured and keyed. The following new species are described :—

Pergamasus (*Pergamasus*) *hortensis* sp. nov.
Pergamasus (*Paragamasus*) *alstoni* sp. nov
cambriensis sp. nov.
cassiteridum sp. nov.
celticus sp. nov.
femoratus sp. nov.
integer sp. nov.
londonensis sp. nov.
longisetosus sp. nov.
minimus sp. nov.
nathistmus sp. nov.
parrunciger sp. nov.
rothamstedensis sp. nov.
schweizeri sp. nov.

The following species are recorded for the first time from Britain : *P.* (*Pergamasus*) *mirabilis* Willm., *P.* (*Paragamasus*) *leruthi* Cooreman, *P.* (*Paragamasus*) *teutonicus* Willm., *P.* (*Paragamasus*) *truncus* Schweizer and *P.* (*Paragamasus*) *wasmanni* (Oudemans).

ACKNOWLEDGEMENTS

I am extremely grateful to Mr. T. E. Hughes for his interest in the work, to the Trustees of the British Museum (Natural History) for providing me with the facilities to work on the material of *Pergamasus* in the collections of the Arachnida Section, and to Dr. G. Owen Evans for his guidance and ready assistance at all times.

My thanks are also due to Dr. J. Cooreman (Brussels) for the loan of type material, to Dr. L van der Hammen (Leiden) for material from the Oudemans Collection, and Prof. A. Melis (Florence) for permission to work on the Berlese Collection. Finally, I have pleasure in expressing my gratitude to the Central Research Funds Committee (University of London) for financial assistance.

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PLATE 1

Armature of leg II in the male of *Pergamasus* s. lat.

a. *Pergamasus* (*Pergamasus*) *crassipes* (L.) Berlese
b. *Pergamasus* (*Pergamasus*) *longicornis* Berlese
c. *Pergamasus* (*Pergamasus*) *septentrionalis* (Oudemans)
d. *Pergamasus* (*Pergamasus*) *quisquiliarum* (Canestrini)
e. Genu & tibia of *Pergamasus* (*Pergamasus*) *quisquiliarum* (Canestrini)

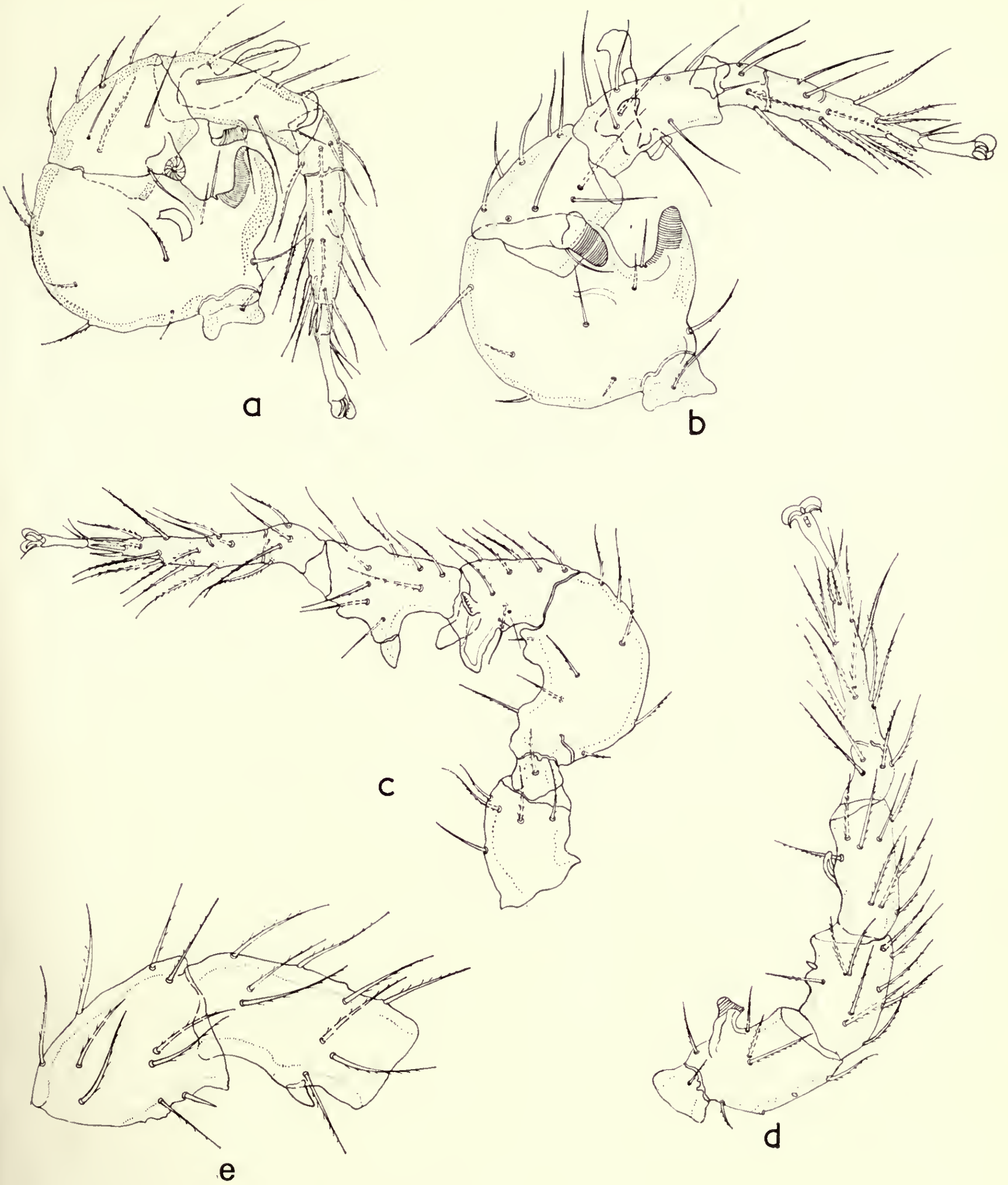
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PLATE 2

Armature of leg II in the male of *Pergamasus* s. lat.

a. Coxa II of *Pergamasus* (*Pergamasus*) *mirabilis* Willmann
b. *Pergamasus* (*Pergamasus*) *mirabilis* Willmann
c. *Pergamasus* (*Pergamasus*) *hamatus* (Koch)
d. *Pergamasus* (*Paragamasus*) *robustus* (Oudemans)
e. Coxa II of *Pergamasus* (*Paragamasus*) *alpestris* Berlese
f. *Pergamasus* (*Paragamasus*) *alpestris* Berlese
g. *Pergamasus* (*Paragamasus*) *armatus* Halbert

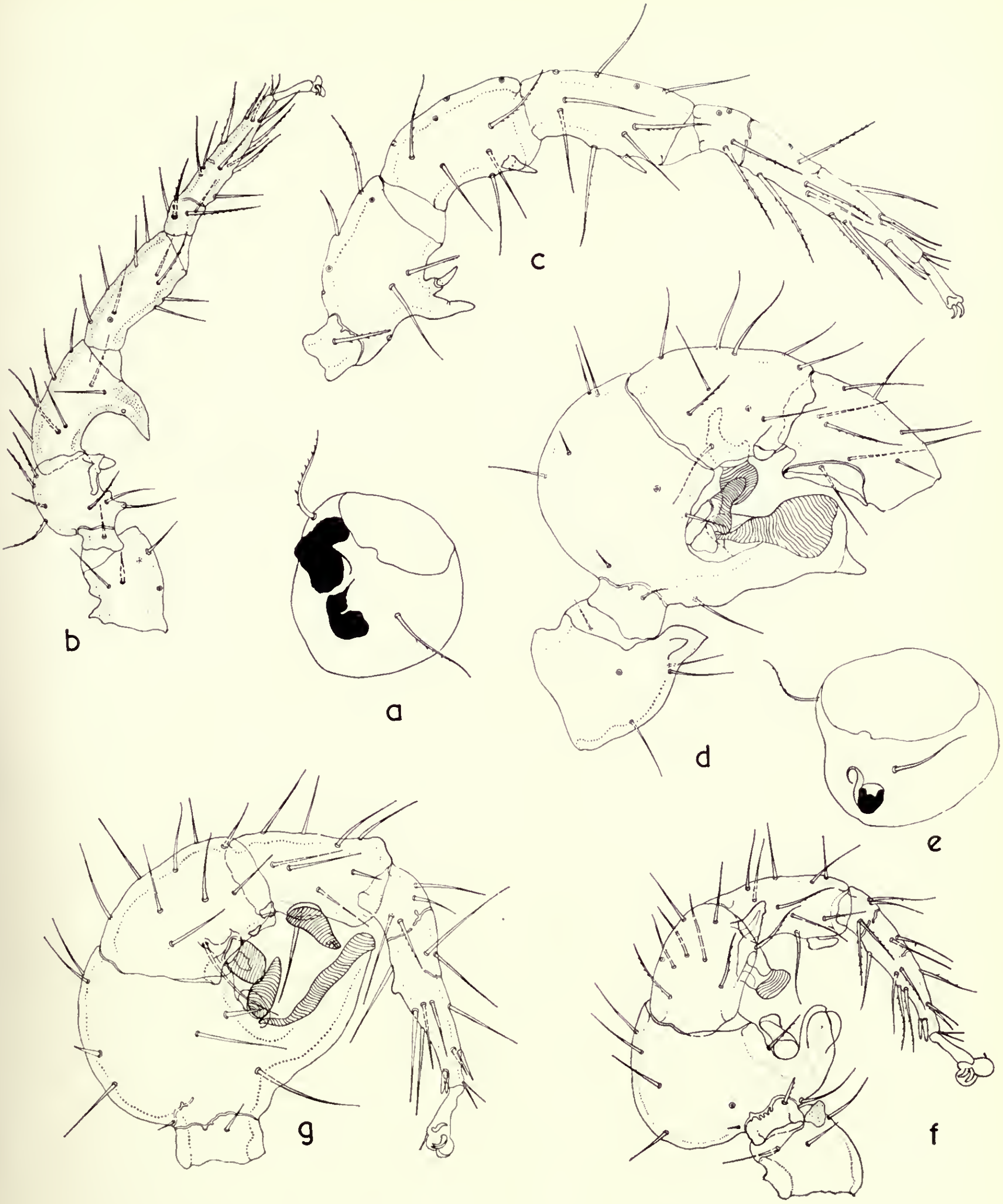
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PLATE 3

Armature of leg II in the male of *Pergamasus* s. lat.

a. *Pergamasus* (*Paragamasus*) *cambriensis* sp. nov.
b. *Pergamasus* (*Paragamasus*) *diversus* Halbert
c. Trochanter II of *Pergamasus* (*Paragamasus*) *cassiteridum* sp. nov.
d. *Pergamasus* (*Paragamasus*) *cassiteridum* sp. nov.
e. Ventral view of femur of leg II in *Pergamasus* (*Paragamasus*) *cassiteridum* sp. nov.
f. Ventral view of femur of leg II in *Pergamasus* (*Paragamasus*) *robustus* (Oudemans)
g. *Pergamasus* (*Paragamasus*) *celticus* sp. nov.

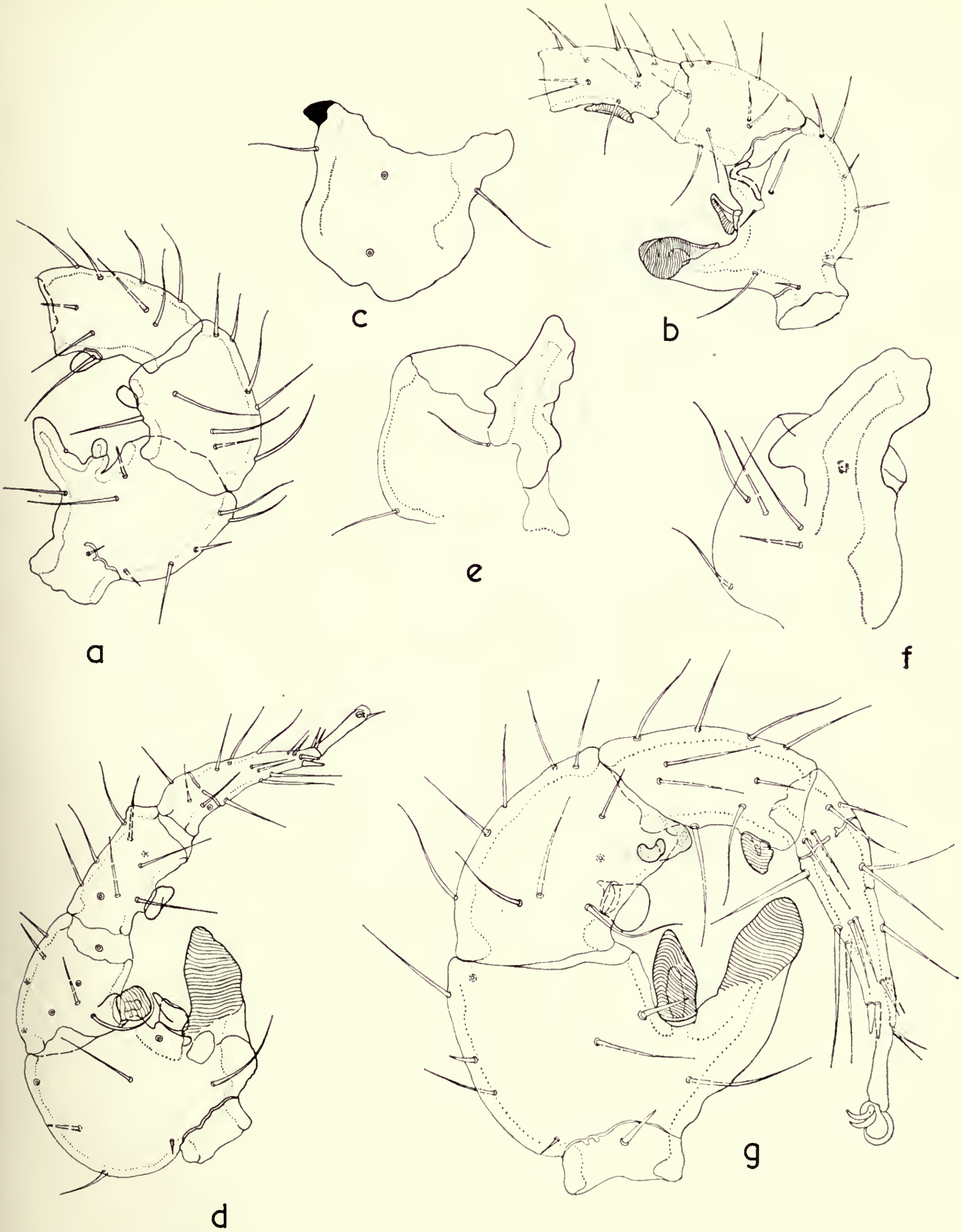
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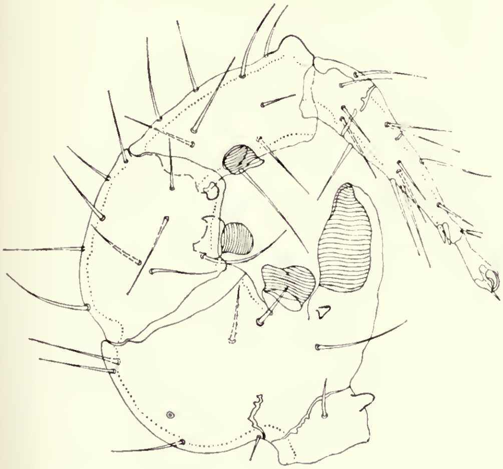
PLATE 4

Armature of leg II in the male of *Pergamasus* s. lat.

a. *Pergamasus* (*Paragamasus*) *femoratus* sp. nov.
b. *Pergamasus* (*Paragamasus*) *integer* sp. nov.
c. Trochanter II of *Pergamasus* (*Paragamasus*) *lapponicus* Trägårdh
d. *Pergamasus* (*Paragamasus*) *lapponicus* Trägårdh
e. *Pergamasus* (*Paragamasus*) *leruthi* Cooreman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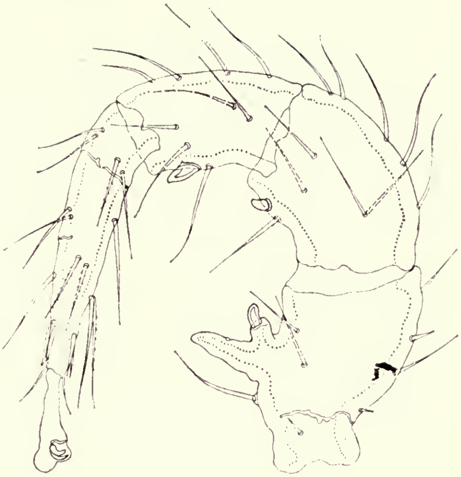
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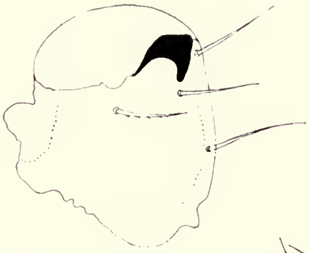
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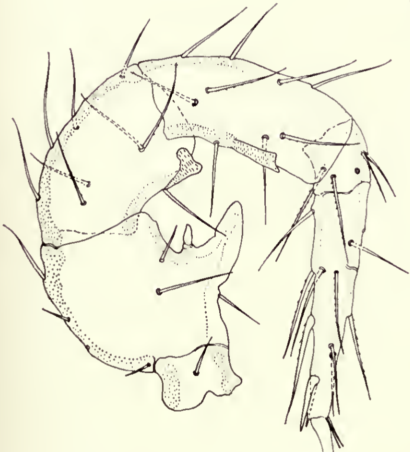
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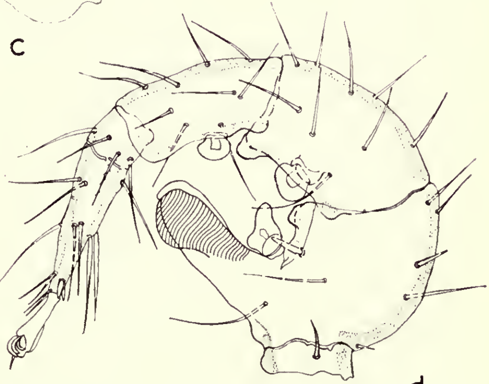
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PLATE 5

Armature of leg II in the male of *Pergamasus* s. lat.

a. *Pergamasus* (*Paragamasus*) *misellus* Berlese
b. *Pergamasus* (*Paragamasus*) *nathistmus* sp. nov.
c. *Pergamasus* (*Paragamasus*) *parrunciger* sp. nov.
d. Variation of tibial spur in *Pergamasus* (*Paragamasus*) *parrunciger* sp. nov.
e. Ventral view of femur in *Pergamasus* (*Paragamasus*) *parrunciger* sp. nov.
f. *Pergamasus* (*Paragamasus*) *rothamstedensis* sp. nov.
g. *Pergamasus* (*Paragamasus*) *runciger* (Berlese)
h. Ventral view of femur in *Pergamasus* (*Paragamasus*) *runciger* (Berlese)

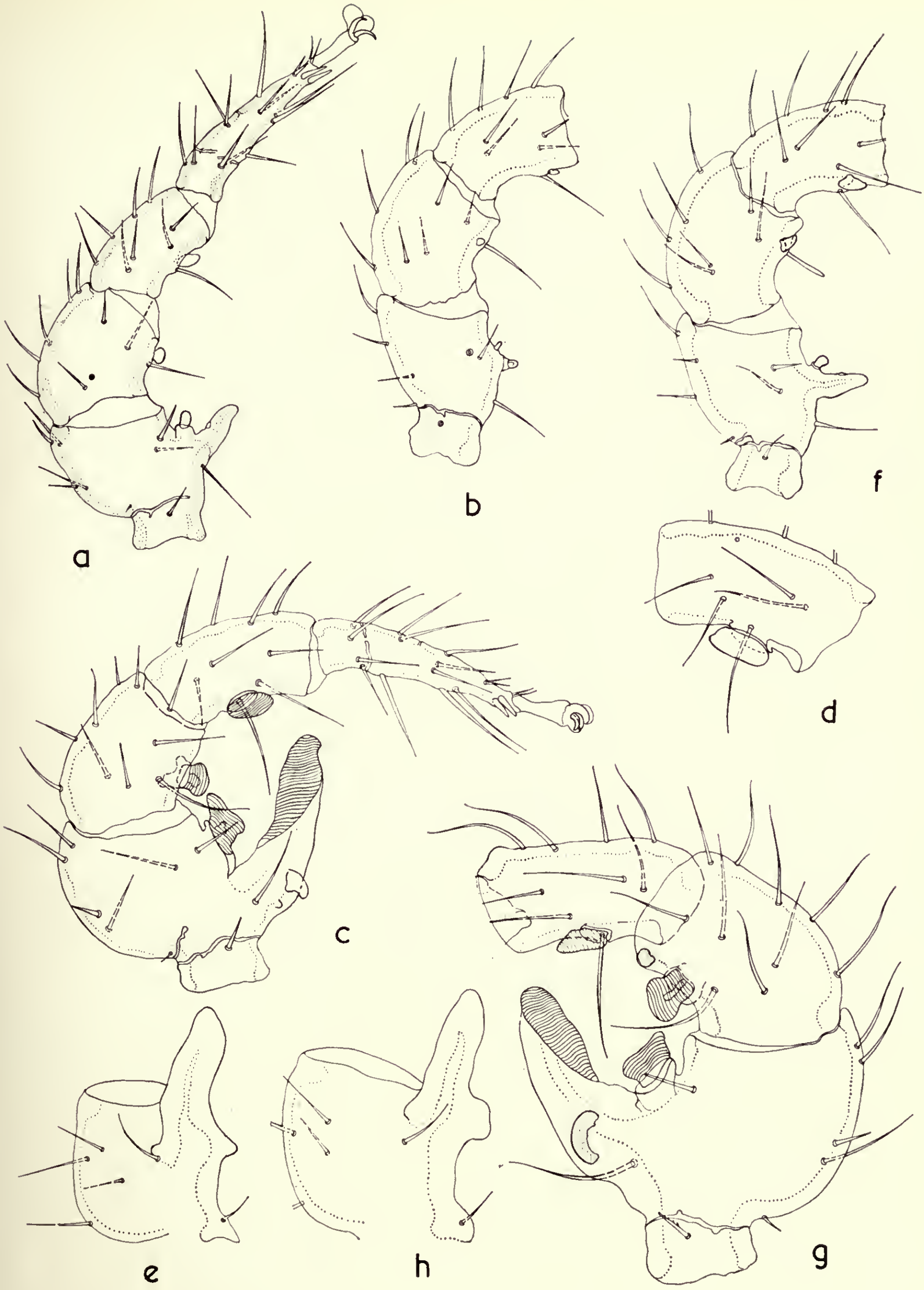
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PLATE 6

Armature of leg II in male of *Pergamasus* s. lat.

a. *Pergamasus* (*Paragamasus*) *schweizeri* sp. nov.
b. *Pergamasus* (*Paragamasus*) *suecicus* (Trägårdh)
c. *Pergamasus* (*Paragamasus*) *teutonicus* Willmann
d. *Pergamasus* (*Paragamasus*) *truncus* Schweizer
e. *Pergamasus* (*Paragamasus*) *wasmanni* (Oudemans)

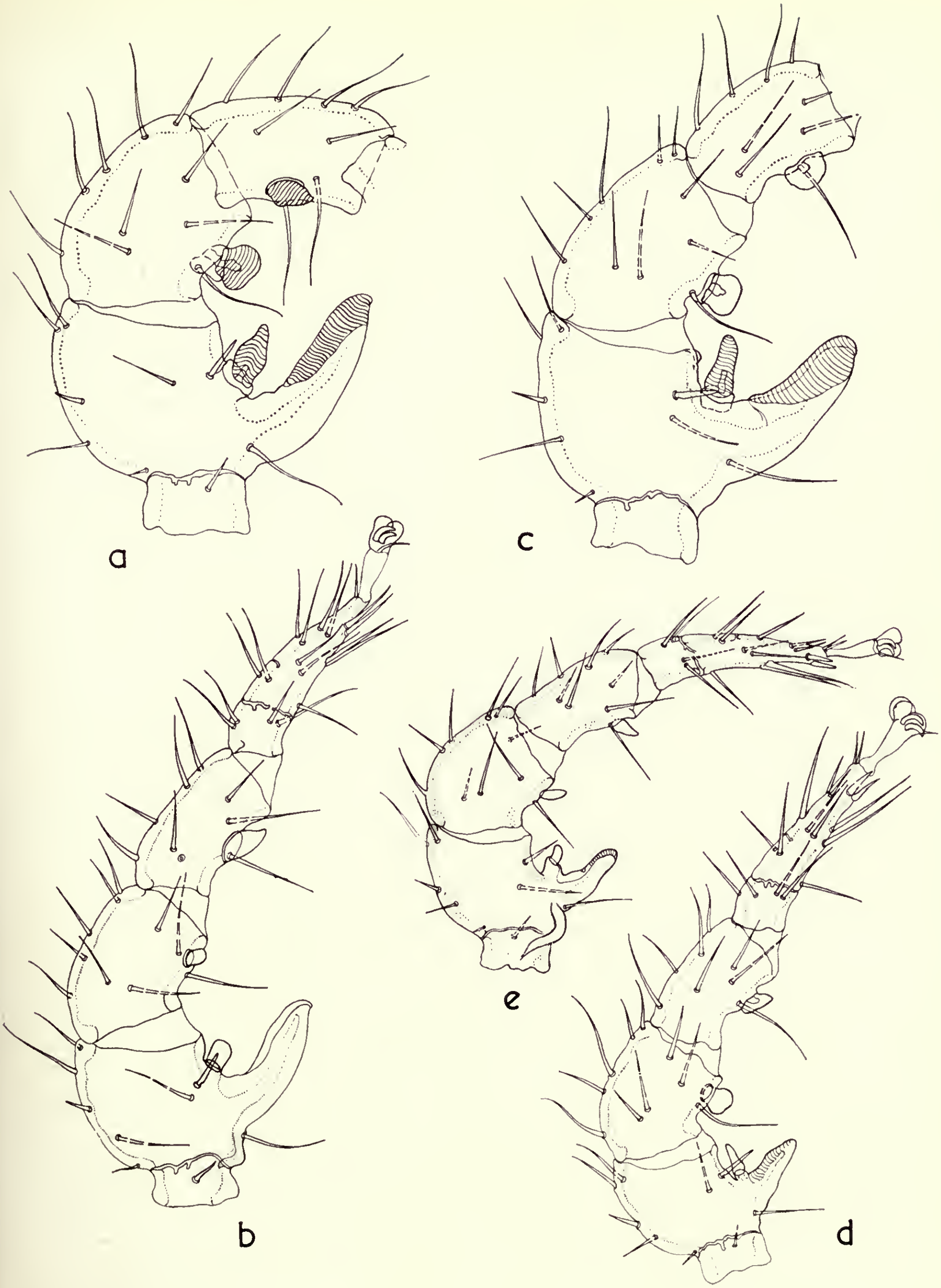
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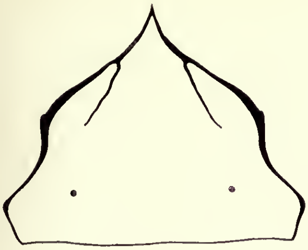
PLATE 7

Genital shields of the females of *Pergamasus* s. lat.

a. *Pergamasus* (*Pergamasus*) *crassipes* (L.) Berlese
b. *Pergamasus* (*Pergamasus*) *longicornis* Berlese
c. *Pergamasus* (*Pergamasus*) *septentrionalis* (Oudemans)
d. *Pergamasus* (*Pergamasus*) *quisquiliarum* (Canestrini)
e. *Pergamasus* (*Paragamasus*) *robustus* (Oudemans)
f. *Pergamasus* (*Paragamasus*) *alpestris* Berlese
g. *Pergamasus* (*Paragamasus*) *alstoni* sp. nov.
h. *Pergamasus* (*Paragamasus*) *diversus* Halbert
i. *Pergamasus* (*Paragamasus*) *integer* sp. nov.
j. *Pergamasus* (*Paragamasus*) *londonensis* sp. nov.
k. *Pergamasus* (*Paragamasus*) *rothamstedensis* sp. nov.
l. *Pergamasus* (*Paragamasus*) *suecicus* (Trägårdh)



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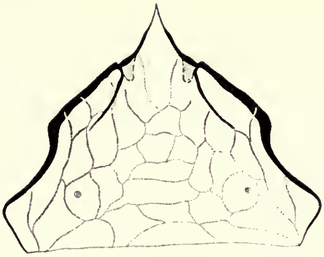

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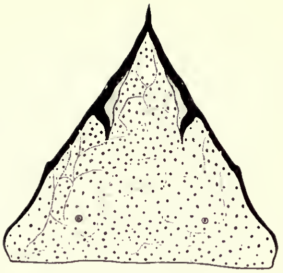

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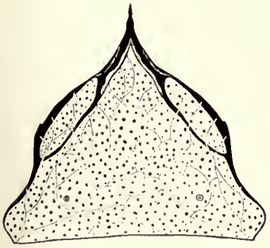

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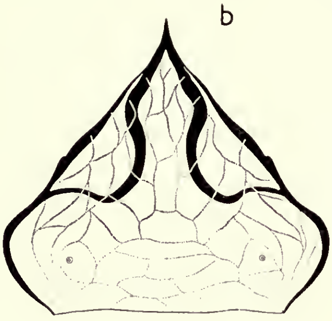

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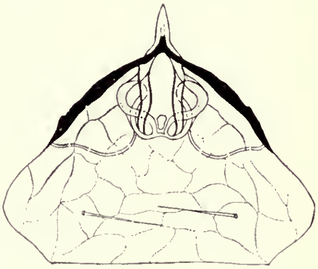

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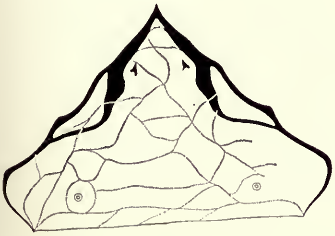

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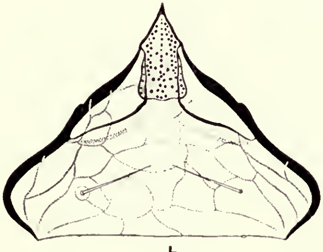

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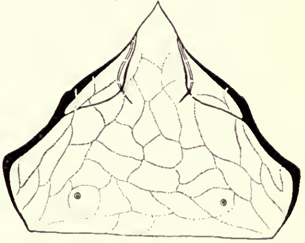

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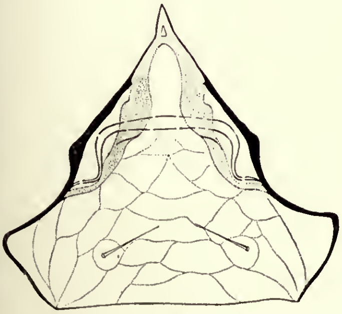

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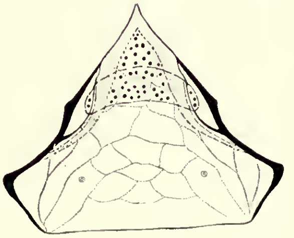

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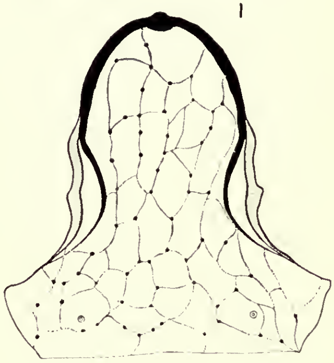

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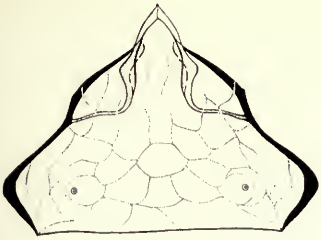
PLATE 8

Genital shields of the females of *Pergamasus* s. lat.

a. *Pergamasus* (*Paragamasus*) *misellus* Berlese
b. *Pergamasus* (*Paragamasus*) *truncus* Schweizer
c. *Pergamasus* (*Paragamasus*) *armatus* Halbert
d. *Pergamasus* (*Paragamasus*) *cambriensis* sp. nov.
e. *Pergamasus* (*Paragamasus*) *wasmanni* (Oudemans)
f. *Pergamasus* (*Paragamasus*) *celticus* sp. nov.
g. *Pergamasus* (*Paragamasus*) *celticus* sp. nov. (internal view)
h. *Pergamasus* (*Paragamasus*) *lapponicus* Trägårdh
i. *Pergamasus* (*Paragamasus*) *lapponicus* Trägårdh (internal view)
j. *Pergamasus* (*Paragamasus*) *parrunciger* sp. nov.
k. *Pergamasus* (*Paragamasus*) *runciger* (Berlese)
l. *Pergamasus* (*Paragamasus*) *schweizeri* sp. nov.
m. *Pergamasus* (*Paragamasus*) *teutonicus* Willmann
n. *Pergamasus* (*Paragamasus*) *teutonicus* Willmann (internal view)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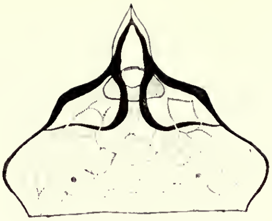
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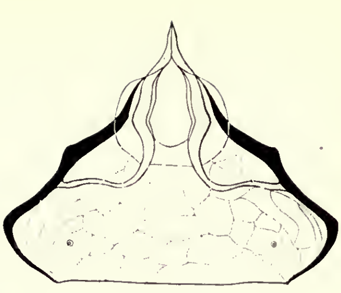
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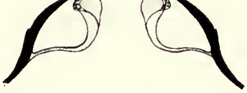
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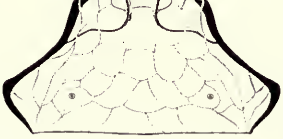
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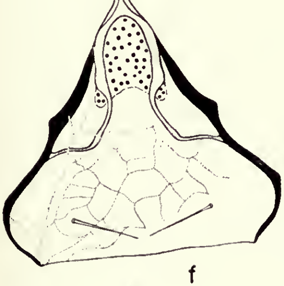
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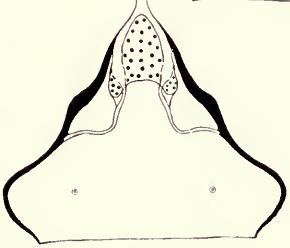
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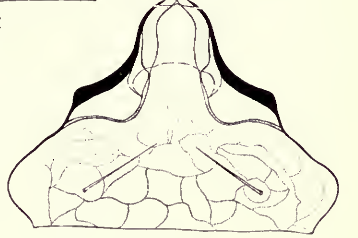
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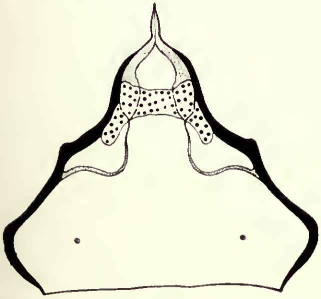
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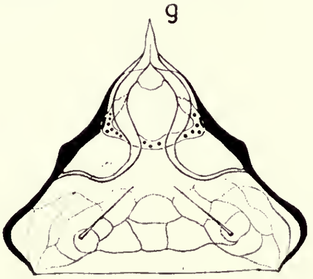
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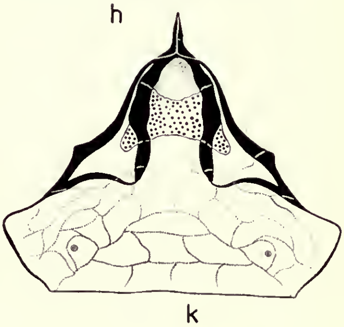
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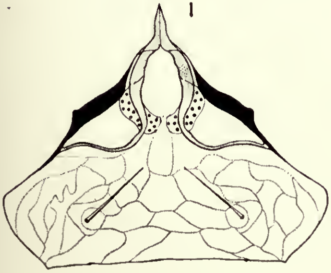
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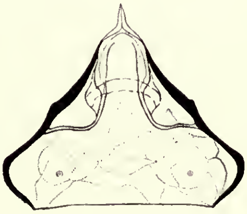
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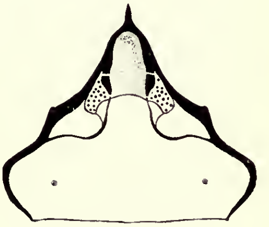
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THE CHEILOSTOMATOUS POLYZOA *NEOEUTHYRIS WOOSTERI* (MacGILLIVRAY) AND *REGINELLA DOLIARIS* (MAPLESTONE)

ANNA B. HASTINGS

BULLETIN OF
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ZOOLOGY Vol. 11 No. 3
LONDON : 1964

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BRITISH MUSEUM
25 FEB 1964
NATURAL HISTORY

BY

ANNA B. HASTINGS
British Museum (Natural History)

Pp. 243–262 ; *Plates* 1–3 ; 4 *Text-figures*

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By ANNA B. HASTINGS

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1. ABSTRACT

Neoeuthyris woosteri (MacG.), unlike the other undoubted members of the Euthyrisellidae (in which ovicells are vestigial or absent), has well developed ovicells. *Urceolipora*, removed from the family by Harmer, has ovicells with some likeness to those of *Neoeuthyris*.

There is evidence of a tendency to reduction of the ovicells of the Cheilostomata, but our knowledge of the factors concerned is still insufficient to frame an explanation.

Metracolposa Canu & Bassler is a synonym of *Reginella* Jullien. *Metracolposa mucronata* Canu & Bassler falls within the range of variation of *Reginella furcata* (Hincks) of which it is thus a synonym.

Cellepora doliaris Maplestone is a member of the Cribrilinidae. Its zooecia have much in common with those of *Reginella*, to which it is tentatively referred. The cribriform frontal shield of its erect zooecia faces the periphery of the low conical colony which is built with a profusion of kenozooecia and avicularia, apparently budded from the septula of the zooecia.

Though belonging to a different major systematic group, the zoarium of *R. doliaris* shows parallel features to that of *Conescharellina* and helps to elucidate the arrangement of the zooecia in the Conescharellinidae.

2. *NEOEUTHYRIS* Bretnall

Neoeuthyris Bretnall, 1921 : 157 ; Hastings, 1960 : 244, 245 ; Opinion 617, 1961 : 363.

Type-species : *Euthyris woosteri* MacGillivray, by monotypy.

The status of the generic name *Neoeuthyris* Bretnall, and of the name of its type-species, was established by Opinion 617 of the International Commission on Zoological Nomenclature. It remains to discuss the material of *N. woosteri* in the British Museum.

2a. *Neoeuthyris woosteri* (MacGillivray)

Text-figs. 1, 2

Euthyris woosteri MacGillivray, 1891 : 77, pl. 9, figs. 2, 2a.

Neoeuthyris woosteri Bretnall, 1921 : 157, text-fig. 1 ; Hastings, 1960 : 244 ; Opinion 617, 1961 : 363.

Distribution : Cooktown, Queensland, on an alga (MacGillivray ; Bretnall) ; Western Australia, on *Metamastophora plana* (Gray ; 1938.8.10.1) ; Fremantle, Western Australia, on part of one of four specimens of *Metamastophora plana*, Harvey's Australian Algae, No. 442 (1948.3.12.1, transferred from Department of Botany).

HOLOTYPE : Cooktown, Queensland, divided between National Museum of Victoria, Melbourne, Victoria (MacGillivray's specimen), and Australian Museum, Sydney, N.S.W. (the rest of the specimen from which MacGillivray's lobe was taken, U.875. Being part of the same specimen this, too, is holotype, not a paratype, c.f. Bretnall, 1921 : 159).

REMARKS : As already noted (Hastings, 1960 : 245), 1938.8.10.1 is the type-material of *Lichenella brentii* Gray (1858), and the algal portion, there chosen as lectotype of Gray's species, is now in the Botanical Department of the British Museum (Nat. Hist.). No intact Polyzoa remain on this lectotype material, though some basal and lateral walls are to be seen. The part including the Polyzoan has been retained in the Zoological Department under the original number.

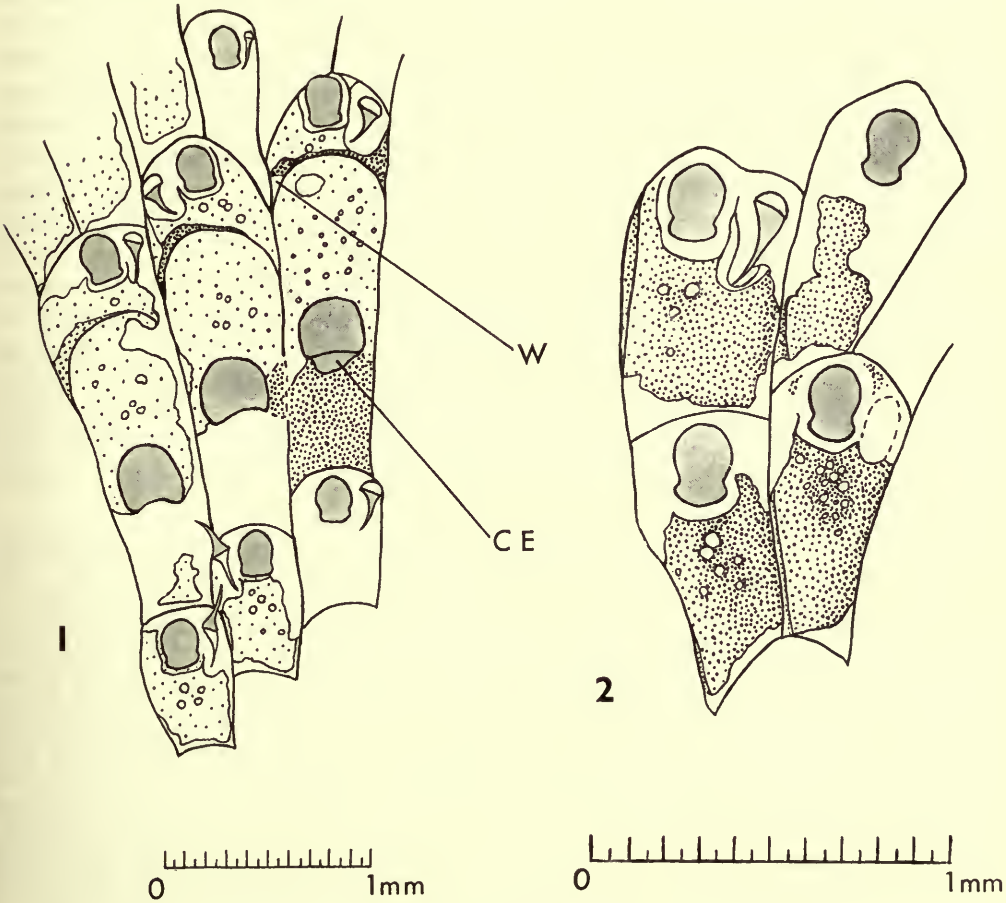
The known colonies of *N. woosteri* all encrust algae and cause a wrinkling of the surface of the encrusted fronds. MacGillivray described the species from a single lobe from a colony whose form was unknown. Bretnall examined the whole, small specimen from which MacGillivray's lobe was taken (Australian Museum, U.875), and established the algal nature of the basal layer. The basal surface, as described by MacGillivray, is like the basal algal layer in Gray's specimen. Miss Elizabeth Pope has very kindly examined the specimen in the Australian Museum, in which one fragment is mounted to show the alga, and she has confirmed the presence of ridges similar to those in Gray's specimen.

No. 442 of Harvey's Australian Algae in the British Museum consists of four specimens of *Metamastophora plana*, one of which bears extensive growths of *Neoeuthyris*. The contrast between the ridged surface of the parts of the fronds bearing the polyzoan, or remains of it, and the smoothness of the colonized parts is striking. It is also interesting to find that a photograph of a specimen which, Mr. Ross tells me, is presumably part of the type-gathering of *Metamastophora plana* shows exactly similar ridges on the fronds (Foslie, 1929, pl. 25, fig. 5).

The colonies of *N. woosteri* are very fragile, being delicately calcified and covered with a thin epitheca which readily breaks away. My material is all old (Gray's specimen has been in the Museum for over a century) and has been dried and preserved between paper as herbarium material. The specimens are therefore considerably damaged. Further, the epitheca may be obscured by a thin growth of a calcareous alga. Fortunately, enough remains intact to show the essential features of the anatomy and the beauty of the species. In fact the damage is sometimes helpful, for zooecia are to be found in which the loss of the epitheca exposes the underlying calcareous parts, others in which the fracture of the calcareous wall exposes the floor of the compensation sac, and others again in which the compensation sac has also been destroyed exposing the interior of the zooecium.

As in *Euthyrisella obtecta* (Hincks), the epitheca is stretched above the depressed, calcareous, frontal wall. It is attached to the raised rim (marginal walls) of the zooecium, the raised rim of the orifice, and the papillae on the frontal wall (Text-fig. 2).

I have not examined the type-material of *Neoeuthyris woosteri* myself, but the species is readily recognizable from the accounts given by MacGillivray and Bretnall, both based on the type-material. The British Museum specimens agree very closely with these accounts, except that they have two types of orifice (Text-fig. 1) resembling the 'A' and 'B' orifices of the other two species of *Euthyris*



FIGS. 1 AND 2. *Neoeuthyris woosteri* (MacGillivray), 1948.3.12.1.

1. Part of the colony, showing three ovicells. Epitheca white, underlying calcareous parts (exposed where epitheca has been lost) lightly stippled, fractures darkly stippled, opercula and mandibles mechanically stippled. *CE*, chitinized proximal extension of operculum ; *W*, bit of frontal wall by ovicell in situ. 2. Four non-fertile zooecia. Epitheca white, underlying calcareous parts (exposed where epitheca has been lost) shaded, opercula and mandible mechanically stippled. On the left side of each zooecium part of the raised rim and the depressed frontal wall of the zooecium can be seen. One complete avicularium and one rudiment (outlined with broken line).

(s. lat.), namely, *Euthyrisella obtecta* (Hincks, 1882a : 165, pl. 7, fig. 3) and *Pleurotoichus clathrata* (Harmer, 1902 : 266, pl. 16, figs. 20, 21). As 'B' zooecia are rather rare in the British Museum material of *Neoeuthyris woosteri*[1] their complete absence from the small pieces of type-material is not surprising, and I am satisfied that the specimens I have examined belong to MacGillivray's species.

The difference between the two kinds of orifice is more marked than in *Euthyrisella obtecta*, as the few 'B' orifices of *Neoeuthyris woosteri* that I have seen are slightly wider and the 'A' orifices are markedly narrower than those of *E. obtecta*. The 'B' orifices of the two species are similar in shape, but the 'A' orifices of *E. woosteri* are somewhat narrowed towards the proximal end and have more pronounced lateral indentations. The latter are well figured by MacGillivray.

Harmer (1902 : 270) remarked that the separate proximal wall of the zooecium in *Pleurotoichus clathratus* "suggests that the 'B' zooecia possess a vestigial ovicell," and his figure (pl. 16, fig. 21) justifies this interpretation. It is therefore interesting to find that the 'B' zooecia of *Neoeuthyris woosteri* bear exceptionally large, fully developed ovicells (Text-fig. 1).

In *Euthyrisella obtecta*, on the other hand, the 'B' zooecia show no trace even of a vestigial ovicell. I have examined the beautiful, stained preparation figured by Harmer (1902, pl. 16, figs. 33, 37, Haddon Coll., Torres Straits, 1916.8.23.115) without obtaining any further evidence as to whether the 'B' zooecia are fertile.

Thus in three species referred to the Euthyrisellidae, all of which have dimorphic orifices, we find *Euthyrisella obtecta* with no ovicells, *Pleurotoichus clathratus* with traces of ovicells, and *Neoeuthyris woosteri* with exceptionally large ovicells, a matter which I discuss further below.

The ovicells of *N. woosteri* are immersed in the zooecium distal to the fertile zooecium. The former are longer and broader than the ordinary zooecia, and the ovicells occupy three-fourths of their length and their whole breadth (Text-fig. 1). In each instance this large zooecium gives rise to two distal zooecia. The ovicell bears a few calcareous papillae like those on the frontal wall. Its lip turns upward to the level of the rim of the zooecial orifice and it is closed by the operculum of the fertile zooecium. The calcareous frontal wall of the zooecium containing the ovicell descends more steeply from the orifice than that of the ordinary zooecia, and ends abruptly against the distal end of the ovicell. Unfortunately, this wall is in every instance more or less broken where it meets the ovicell. One small piece has, however, remained in its proper position in the right-hand figured zooecium (Text-fig. 1, W). The epitheca of the zooecia containing the ovicells is much damaged, but sufficient remains on the left-hand ovicell in Text-fig. 1 to show that it extended over the frontal surface of the zooecium at the usual level without moulding itself to the contours of the underlying descending wall and ovicell.

The ovicellular (B) operculum has a chitinized, proximal extension (Text-fig. 1, CE) behind the proximal sclerite. The figured example is incomplete : when undamaged this extension is wider and symmetrical.

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[1] There are three in 1948.3.12.1 (see fig. 1) and five in 1938.8.10.1.

Bretnall (1921 : 159) suggested that the specimen of *Euthyris* mentioned by Levinsen (1909 : 273, obtained from Mr. C. N. Peal) may have belonged to *Neoeuthyris woosteri*. I have been unable to trace Mr. Peal's specimen.

N. woosteri is not included in Livingstone's check-list of Queensland Polyzoa (1927).

Generic Position : All the three species discussed above were referred at first to *Euthyris* Hincks (1882a : 164, type-species *E. obtecta*). This name is preoccupied by *Euthyris* Quenstedt (1869 : 442, 718), a genus of Brachiopoda. Bassler (1936 : 161) introduced *Euthyrisella* to replace it.

MacGillivray regarded his species as congeneric with *Euthyrisella obtecta*. Harmer (1902 : 268) doubted whether they were congeneric (there is no evidence that he had seen a specimen of MacGillivray's species) ; and Bretnall, after examining MacGillivray's type-material, considered that it was generically distinct, and made *Euthyris woosteri* the type of a new genus *Neoeuthyris*. He based this opinion chiefly on the absence of dimorphism of the orifices, a distinction which we now know to be invalid, and on the presence of avicularia.

Neoeuthyris woosteri resembles *Euthyrisella obtecta* in the relation of the epitheca to the underlying, calcareous frontal wall, in the presence of a few calcareous papillae on this frontal wall proximally to the orifice (cf. Harmer, 1902, pl. 16, fig. 32), and in possessing orifices of two kinds. I have not seen pores, except for one or two small ones which may be present in the wall of the avicularian chamber near its junction with the frontal wall. *Neoeuthyris woosteri* differs from *Euthyrisella obtecta* in the presence of avicularia (well figured by MacGillivray), in the presence of ovicells, and in the colony which is encrusting and without the basal papillae and raised basal epitheca found in *E. obtecta*.

These differences together may justify the generic separation, but individually none of them is of great significance. The presence or absence of avicularia, and the form of the colony are generally recognized as frequently not of generic significance, and I have given evidence below that the presence or absence of ovicells may also be unimportant generically. On the other hand, the close similarity of the frontal wall to that of *Euthyrisella obtecta* with its papillae and raised epitheca, and the general resemblance of the 'A' and 'B' zooecia are important points of resemblance. If *Neoeuthyris woosteri* and *Euthyrisella obtecta* are congeneric, the name *Euthyrisella* becomes a synonym of the earlier *Neoeuthyris*.

Bretnall quoted the definition of the Euthyridae[1] given by Levinsen (1909 : 269), who included *Urceolipora* MacGillivray in the family and therefore mentioned the ovicells of that genus in the definition. Levinsen (p. 271) described these ovicells as " of a most peculiar structure, being endozooecial and at the same time having their endooecium situated frontally to the cryptocyst of the zooecium, which is much excavated to receive its arched basal surface ". His description and figure appear to be accurate,[1] but his interpretation of the structures seen is puzzling.

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[1] Replaced by Euthyrisellidae by Bassler (1953 : G226). If *Euthyrisella* were regarded as a synonym of *Neoeuthyris* no further change of family name would be necessary according to Article 40, Rules of Zoological Nomenclature, 1961 : 41.

The relationship of the ovicell of *Neoeuthyris* to the flat frontal membrane and descending calcareous wall of the distal zooecium suggests comparison with *Urceolipora*, but it is possible that the calcareous wall does not extend beneath the ovicell. The point is important in determining whether *Urceolipora* should be separated from the Euthyrisellidae (see Harmer, 1957 : 874), but fresh material of *Neoeuthyris* is needed before it can be settled.

3. REDUCED AND VESTIGIAL OVICELLS

I hope to discuss some of the problems concerning the ovicells of the Cheilostomata in another paper, but the marked differences in the brooding arrangements among the Euthyrisellidae, noted above, need some comment here.

There is increasing evidence that, although the structure of the ovicells, when present, may be of considerable taxonomic significance, their presence or absence is sometimes not even a generic character. Levinsen (1909 : 72) commented on this, but my attention was particularly drawn to it by the comments of Harmer (1926), who recorded a number of pairs of species in which one member of the pair has a well developed ovicell, and the other, while very similar in other respects, has a shallow ovicell incapable of accommodating the embryo ; or no ovicell at all, the embryo then occupying a sac in the body-cavity. Examples of such pairs are :— *Carbasea linguiformis* and *C. pedunculata* (pp. 249, 250), *Retiflustra cornea* and *R. schönaui* (p. 253), *Farciminellum alice* and *F. atlanticum* (p. 405), *Bugula johnstonae* and *B. longicauda* (p. 451), and, among the Ascophora, *Tetraplaria ventricosa* (Haswell) and *T. immersa* (Haswell), see Harmer (1957 : 1053, 1055).

I have examined several similar instances, notably *Umbonula ovicellata* and *U. littoralis* (see Hastings, 1944 : 273, 274), *Crassimarginatella exilimargo*, *C. marginalis* and *C. spatulifera* (see Hastings, 1945 : 78, 84), *Carbasea papyrea* and *C. carbasea* (see Norman, 1903 : 582. *C. solanderi* Norman = *C. carbasea*).

Cornucopina polymorpha and *C. infundibulata* (see Hastings, 1943 : 397, 399) are of especial interest because the well developed ovicells of the one species and the shallow ones of the other are both borne on special, small zooecia which are not found in other species of the genus, and there are thus particularly strong reasons for thinking that the two species are very closely related.

Harmer (1926 : 411 *et seq.*) noted less closely paired examples in *Beania* ; while *Himantozoum*[2] (see Hastings, 1943 : 423) shows a gradation from the species with fully formed ovicells to species in which the fertile zooecia show little or no trace of an ovicell. The gradation of the ovicells of *Camptoplites* (see Hastings, 1943 : 436, etc.) and *Bugula* (Hastings, MS) are interesting in this connection. See Addendum.

The members, hitherto known, of a certain group of species of *Bugula* all have distinctive, globular, obliquely placed ovicells. Ryland (1963 : 23) has recently described a new species, *B. gautieri*, agreeing with this group in other respects, but having extremely vestigial, symmetrically placed ovicells, and an internal ovisac.

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[1] Harmer (1957, text-fig. 94, p. 874) gave a figure of *U. nana* which appears to differ from Levinsen's in the relationship of the ovicell to the calcareous frontal wall (Levinsen's cryptocyst). The figure is, however, diagrammatic and simplified, and the specimen on which it was based (Cambridge Museum, reg. May 13, 1899) agrees with Levinsen's figure.

[2] Silén (1951 : 63) made the illuminating suggestion that this genus appears to be more nearly related to the Farciminariidae than to the Bicellariellidae with which it has hitherto been placed.

In the examples so far mentioned the differences in the ovicells are specific. Some pieces of *Crassimarginatella spatulifera* Harmer (1926 : 223), collected off Formosa (119° 35′ E, 23° 32′ N) by Prof. T. Y. H. Ma (1961.2.20.2) are of particular interest in showing a range of variation in the development of the ovicells within the one sample of one species, and, indeed, within the individual fragments. Some of the ovicells are fairly prominent, rounded and immediately recognizable as ovicells, though shallow. At the other extreme, the slight modification of the distal end of the zooecium, which is all there is to represent the ovicell, deserves to be called vestigial (c.f. Harmer, 1926, pl. 14, fig. 2).

Among the members of the Euthyrisellidae discussed in this paper the instance of *Euthyrisella obtecta* and *Neoeuthyris woosteri* (which are so much alike in many ways, and may be congeneric) is particularly striking.

It will be noticed that the examples quoted include some pairs in which the well-developed ovicell is hyperstomial, and others where it is endozooecial. The small ovicells are usually called reduced or vestigial. The latter term should perhaps be reserved for the extreme cases where the external structure would hardly be recognized as an ovicell were it not for the evidence of the internal ovisac, see, for example, *Bugula longicauda* Harmer (1926 : 450, pl. 30, fig. 15). In some instances Harmer has put forward the view that an evolutionary reduction is responsible (e.g. Harmer, 1926 : 405). It is certainly hard to imagine that the fully developed ovicells of the various genera could have been evolved independently and reached their similarity by convergence.

It is difficult to find any explanation of this tendency to reduction of the ovicells. In considering the pairs of species, I noted the depths at which the various pairs have been found, but no constant relationship was to be observed ; nor is any general geographical or climatic correlation discernible. The examples mentioned are from localities throughout the world and with very diverse climates.

In the European pairs mentioned (*Umbonula ovicellata* and *U. littoralis*, and *Carbasea papyrea* and *C. carbasea*) the species with the internal ovisacs has a more northerly range than the one with ovicells ; but there are *Umbonula* species farther north which reverse this relationship.[1]

Carbasea carbasea and *C. papyrea*, on the other hand, appear to be an example of a more general north and south (arctic or boreal and mediterranean) pairing, not specially associated with brooding arrangements, nor peculiar to the Polyzoa. Nordgaard (1918 : 92, 95), discussing the distribution of the arctic and Norwegian Polyzoa, listed several such instances among which the northern *Porella compressa* (Sowerby) and the mediterranean *P. cervicornis* (Pallas) are a well-known pair. Nordgaard wrote (p. 95) that he had come to the conclusion that there is a dualism in the species of northern animals. " To a southern form there is often a nearly related northern, to a tertiary species there may be commonly found a quaternary pendant." In a valuable zoographical discussion, he tried to relate this dualism to the effect of the cooling northern climate on a warm-water (mediterranean-type) Tertiary fauna. Unfortunately the palaeontological data are not yet adequate, though the revision of the Pliocene Polyzoa of the Low Countries by Lagaaij (1952) provides much useful information.

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[1] *U. ovicellata* (Mediterranean to S.W. Britain) : ovicells. *U. littoralis* (English Channel to Norway and Denmark) : no ovicells. *U. arctica* (Boreal and Arctic) : no ovicells. *U. patens* (Arctic) : ovicells. (See Hastings, 1944 : 277, 282, and Osburn, 1952 : 298, 299).

Borg (1933 : 141) also noted north and south pairing of Polyzoan forms, but within the boreal and arctic zones. He stated that not a few species designated as boreal or arctic-boreal are vicariously replaced in the true Arctic by more or less distinct varieties or by species. He listed 21 examples. Again there is no correlation with brooding arrangements.

Much more knowledge of the ovicells themselves, and also of these more general examples of pairs of species, is needed before an explanation of the observed tendency to reduction of polyzoan ovicells can be attempted. In the meantime one can only draw attention to the problem.

4. ***REGINELLA*** Jullien

Reginella Jullien, 1886 : 605 ; Canu, 1900 : 446 (as a subgenus of *Cribrilina*) ; Canu & Bassler, 1920 : 283 ; 1929 : 243 (English translation of Jullien's definition) ; Osburn, 1950 : 178 ; Brown, 1958 : 52.

Metracolposa Canu & Bassler, 1917 : 34 ; 1920 : 283, 304 ; Osburn, 1950 : 179.

TYPE-SPECIES of *Reginella : Cribrilina furcata* Hincks, 1882b : 250 ; 1882c : 470, pl. 20, fig. 5. Figure reproduced in Canu, 1900 : 446, text-fig. 61, and Canu & Bassler, 1920 : 282, text-fig. 18N. Recent, Queen Charlotte Islands.

TYPE-SPECIES of *Metracolposa : Metracolposa robusta* Canu & Bassler, 1917 : 35, pl. 3, fig. 6. Figure reproduced, 1920, pl. 43, fig. 3. Eocene, North Carolina.

Jullien apparently introduced his genus on the basis of Hincks's figure. This shows the lacunae (intercostal spaces) occupying polygonal areas, and Jullien accordingly included this character in his generic definition, which has been translated and quoted. Hincks does not mention these areas, and they are not shown in Osburn's figures. In the British Museum specimen (1886.3.6.17–18) some of the intercostal connexions are markedly convex, like the costae. The lacunae are then at the bottom of a series of regular hollows which, in certain lights, appear to be outlined ; but this can readily be shown to be no more than an effect of light and shade.

Osburn redescribed *R. furcata*, and referred certain other species to the genus. He suggested that *Metracolposa* might be synonymous with *Reginella*, from which it differs in its escharan colony and in possessing avicularia. I think he was right. I have not seen a specimen of the type-species of *Metracolposa*, but in view of the very close similarity of its zooecia and ovicells to those of *Reginella*, I cannot regard its escharan colony and the presence of avicularia as distinguishing it generically. Interzooecial communication by means of septula has been recorded for the type-species of both genera (Osburn, 1950 : 179 ; Canu & Bassler, 1920, pl. 43, fig. 6). The zooecial operculum closes the ovicell in *R. furcata* and Canu & Bassler deduced (from the hard parts of the fossil type-species) that it also did so in *Metracolposa*.

Waters (1904 : 42) noted agreement between his antarctic species, *Cribrilina projecta*, and *Reginella*. Brown (1958 : 53) considered that *C. projecta* and certain other species discussed by him " are evidently congeneric with *Reginella furcata* ". My own study (unpublished) of the specimens of *Cribrilina projecta* in the collections of the Discovery Investigations, as well as Waters's type-material, indicates that this species is not congeneric with *Reginella furcata*.

4a. ***Reginella furcata*** (Hincks)

Cribrilina furcata Hincks, 1882b : 250 ; 1882c : 470, pl. 20, fig. 5 ; O'Donoghue, 1923 : 172 ; Waters, 1924 : 609, pl. 19, fig. 5 (ancestrula).

Reginella furcata Jullien, 1886 : 605 ; O'Donoghue, 1925 : 101 ; 1926 : 98 ; Osburn, 1950 : 179, pl. 28, fig. 3 ; Androsova [1960?] : 44, 59, pl. 1, fig. 4

Metracolposa mucronata Canu & Bassler, 1923 : 92, pl. 35, fig. 4.

Reginella mucronata Osburn, 1950 : 180, pl. 28, fig. 4, pl. 29, fig. 3 ; Soule & Duff, 1957 : 104 ; Soule, 1959 : 46 ; Hertlein & Grant, 1960 : 86 (record only).

DISTRIBUTION : Recent. Pacific coast of America from Queen Charlotte Islands to Lower California (see Osburn and Soule) ; Yellow Sea (Androsova). Fossil. Pleistocene and Pliocene, California (see Soule & Duff and Hertlein & Grant).

MATERIAL EXAMINED : 1886.3.6.17, 18, Queen Charlotte Is., presented by the Geol. & Nat. Hist. Survey of Canada and determined by Hincks. 1921.11.17.12, Departure Bay, Vancouver Is., B.C., presented and determined by Dr. C. H. O'Donoghue.

REMARKS : If *Metracolposa* were retained as a distinct genus, *M. mucronata* Canu & Bassler, which is not known to have avicularia and is encrusting, would still have to be placed in *Reginella*, where Osburn placed it. He recognized it as closely akin to *R. furcata*. According to his key and description, they agree in the general characters of the frontal shield, in the ovicell and ancestrula, in their dimensions, and in the absence of avicularia ; they differ in the presence of oral spines in *R. furcata* (absent in *R. mucronata*), in the proximal lip of the aperture (apertural bar in key, p. 179) which is described (p. 181) as " stronger and more or less bimucronate " in *R. mucronata*, and in the more variable number of lumen pores in *R. furcata* (2–4 oval pores compared with 2 small round pores in *R. mucronata*).

I think, however, that these distinctions do not hold. Osburn has himself remarked (p. 181) that the spines are often " wanting " in *R. furcata ;* and Hincks described and figured " a peristome rising in front to a central mucro ". The Queen Charlotte Island specimen of *R. furcata* in the British Museum shows considerable variation in the apertural bar. It may be unthickened or thickened, non-mucronate or with a mucro of variable form, in one instance slightly bifid. O'Donoghue's specimen has more of the zooecia with a thickened, mucronate bar, and the mucro is often bifid (" bimucronate ") as in *R. mucronata*, but the specimen has oral spines. Osburn figured the costae as completely transverse in *R. furcata*, but radiating proximally in *R. mucronata*. In this, however, the British Museum material of *R. furcata* and Canu & Bassler's figure of *R. mucronata* both show variation.

The zooecial operculum closes the ovicell in *R. furcata*, but according to Canu &

Bassler's description it did not do so in *R. mucronata*. There seems, however, to be nothing to indicate such a difference between *R. mucronata* and *R. robusta* (see above), so I think that their statement must have been a slip, and that both of these fossil species probably agreed with *R. furcata* in this respect. Osburn did not mention this character in his descriptions of *R. furcata* and of the recent material which he referred to *R. mucronata*.

The evidence thus indicates that *R. mucronata* is a synonym of *R. furcata*.[1]

One of O'Donoghue's colonies of *R. furcata* (1921.11.17.12) has an ancestrula, and shows, in comparison with Waters's figure of a specimen from British Columbia, that there is some variation in the details of the early stages of the colony. O'Donoghue's ancestrula has 13 marginal spines (Waters showed 10), and it has given rise to only 2 zooecia distally. It has 2 small distal spines (one represented by its base only), 5 moderately erect lateral spines (or remains of spines) on each side, and the base of a median, proximal spine. The first two zooecia have each formed a pair of distal buds, and, by continued budding, a fan-shaped colony has been produced.

The pointed structures in, or over, the orifice in the figure given by Androsova (1960? pl. 1, fig. 4) are presumably the forked spines, c.f. Osburn (1950, pl. 28, fig. 3).

4b. ***Reginella doliaris*** (Maplestone)

Pl. 1, figs. 1–3, pls. 2, 3

Cellepora doliaris Maplestone, 1909 : 272, pl. 77, figs. 10 a, b.
Reginella doliaris Brown, 1958 : 53.

MATERIAL EXAMINED : One dry colony, marked " co-type," 1909.11.12.14, 22 miles E. of Port Jackson, c. 80 fms. (the only known locality), presented by the University of Sydney, N.S.W.

DESCRIPTION : *Zoarium* (pl. 1, figs. 1–3) apparently free, low conical, with concave, oval base with axes *c.* 3·5 and 3 mm., the zooecial orifices on the convex surface, their proximal ends at the concave surface, the thickness of the zoarium at the edge being the length of the zooecia (pl. 1, fig. 3, pl. 3, figs. 1, 2, 5). Small chambers (interpreted as kenozooecia), with finely granular walls, occupying the interstices between the zooecia laterally and on the convex surface of the colony, and filling the concavity (pl. 2, fig. 1, pl. 3, figs. 1–5). Avicularia frequent on both surfaces.

Zooecia erect, with cribrimorph frontal shield, this frontal wall facing the periphery of the zoarium, the proximal end of the zooecium rounded without distinction of proximal from lateral walls (pl. 3, figs. 4, 5), orifice in a plane oblique to that of frontal shield.

Frontal shield (pericyst[2]) *c.* 0·1 mm. × 0·5 mm. with 9–13 regular costae with an even series of small lacunae between them (pl. 3, fig. 1), costae transverse except proximally where they radiate, the apertural bar stout, in the best preserved zooecia rising to a short blunt median point (pl. 3, fig. 3), elsewhere more or less worn, appearing irregular, occasionally denticulate, or smooth.

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[1] I have not considered the validity of the other species recognized by Osburn.

[2] *Frontal shield*, term introduced by Harmer, 1902 : 282 footnote.
Pericyst, synonymous term, introduced by Canu & Bassler, 1929 : 115 footnote.
For definitions of these and other terms see Bassler's valuable glossary (1953 : G7–G16).

Orifice nearly circular with very slight constrictions marking off a deep anter from a shallow poster.

Oral spines four, erect, broad, flattened, slightly bifid (pl. 2, fig. 2) ; distal pair fused to form a distal plate,[1] the suture, visible as a groove on the outer surface[2] of the plate, running from a small pit at the base, this little hollow visible when rest of suture obliterated ; outer spines beside orifice, somewhat curved, taller than the plate and touching it laterally ; spines and plate partially or completely worn away in older zooecia.

Operculum presumably delicate, not articulating with the frontal shield (shrivelled remains sometimes visible within the orifice at a deeper level than the apertural bar).

Septula in a regular row just below the bases of the costae (pl. 3, fig. 4), extending round proximal end of zooecium, generally hidden by kenozooecia.

Kenozooecia developed as a linear series along lateral walls and round proximal end of each zooecium (pl. 3, figs. 1, 2), apparently originating from the septula.

Avicularia commonly (but not on every zooecium) replacing a distal lateral kenozooecium on one or both sides of a zooecium, and also the median proximal kenozooecium (pl. 3, fig. 1). As more zooecia develop, these avicularia come to lie on the two surfaces of the colony, those on the convex surface (pl. 2, fig. 1) lying beside the orifice at a little distance from it (this follows from their development as distal members of the lateral series of kenozooecia), the proximal ones mingling with the kenozooecia filling the concavity (pl. 1, fig. 3). Avicularian chambers prominent, rounded, somewhat tapering proximally to give " cornucopia-shape " described by Maplestone. Beak strong and very bluntly pointed. Mandible a rounded, nearly equilateral triangle, articulated to condyles.

Ovicells not found.

Remarks : In the younger parts of the colony the zooecia are immersed so that little more than the border of the orifice (apertural bar, spines and distal plate) projects at the surface of the colony, but a few zooecia (in particular three at the apex) project further showing part of the cribriform wall (pl. 1, fig. 2, pl. 2, fig. 1). One of the apical ones has this wall exposed for about half its length. These apical zooecia show the extremely abraded condition in which the spines and distal plate are worn right down to their base, and the apertural bar is also worn smooth.

There is only one point where there is any trace of an incomplete zooecium. It takes the form of a low, curved, proximal wall applied to the cribriform surfaces of two neighbouring zooecia (pl. 3, fig. 5). These zooecia overlie each other in such a way that the lateral kenozooecia of one zooecium are applied to the frontal wall of the one partially covered by it (pl. 3, figs. 1, 2, 5). The zooecial rudiment lies mostly on the underlying zooecium, and appears to originate from one of the more proximal members of the lateral series of kenozooecia of the upper zooecium. The arrangement of the zooecia in the colony indicates that the position of this bud represents the usual point of origin of the new zooecia.

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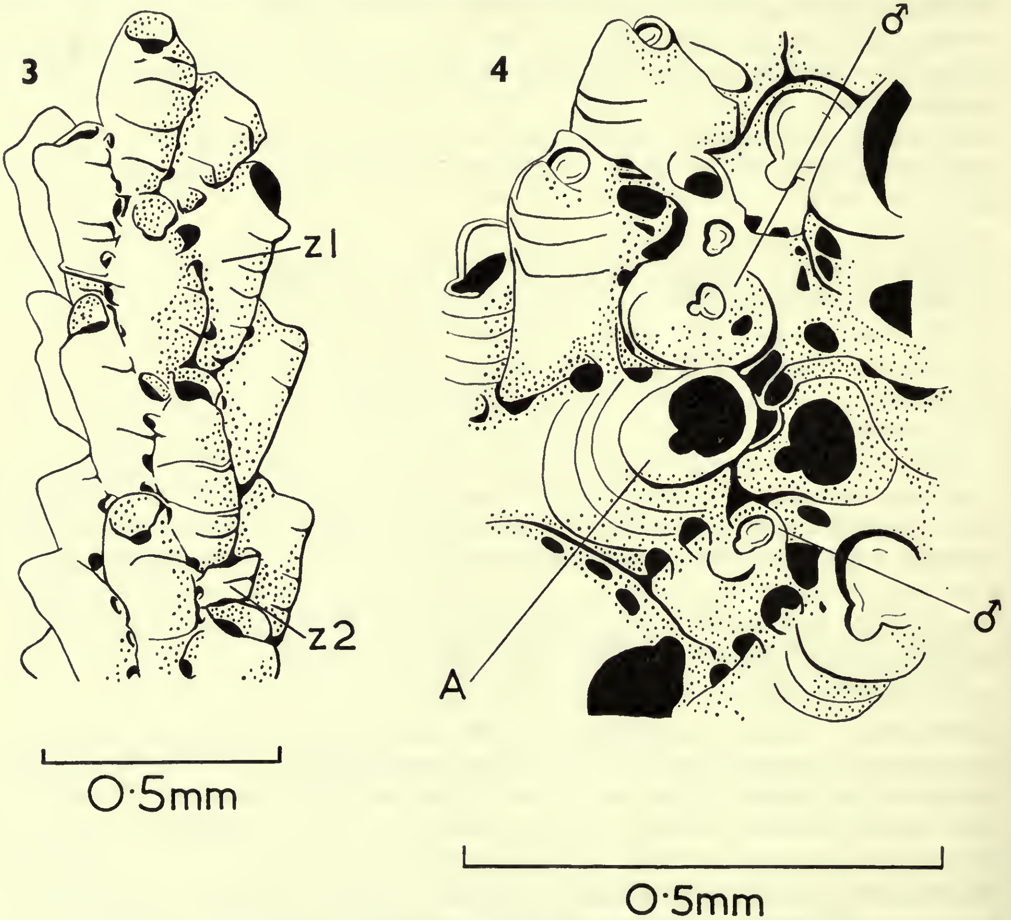
[1] The term *distal plate* was used by Lang (1916 : 82 ; 1921 : 46–47) for similar structures in Cretaceous Cribrimorph Polyzoa.

[2] *Outer surface*, i.e. the surface away from the orifice.

The relation to each other of the various kinds of zooecia in the colony of *Hippothoa hyalina* (s. lat.) is sometimes strictly comparable to that of the zooecia of *Reginella doliaris*, as just described. For example, Marcus (1938, pl. 20, fig. 56) showed the



FIGS. 3 AND 4. *Hippothoa* sp. False Bay, South Africa, 1963.1.12.1.

3. Recumbent zooecia showing chambers along the interzooecial grooves, and the beginning of the growth of superficial layers. *z*1, complete zooecium overlapping frontal surface of two neighbouring zooecia ; *z*2, proximal part of incomplete zooecium applied to the frontal surface of another zooecium. 4. Erect, jumbled growth showing male zooecia applied to frontal surface of asexual zooecia, and also the converse relationship. ♂, male zooecium applied to asexual zooecium ; *A*, asexual zooecium overlapping two male zooecia and another asexual zooecium. Drawings by Miss P. L. Cook.

sexual zooecia arising in the interzooecial grooves and applied by their basal surface to the frontal surface of the neighbouring asexual zooecia. The asexual zooecia may also be applied to the frontal surface of their neighbours in the same way. In a specimen of *Hippothoa* sp. from South Africa (False Bay, 1963.1.12.1), which shows these features well, they even overlie the small male zooecia. In the younger portion of the specimen the zooecia are recumbent, with a series of distinct chambers (areolar? kenozooecial?) along the interzooecial grooves, and a superficial layer just beginning to form (Text-fig. 3, c.f. Osburn, 1933, pl. 9, figs. 1, 2). The zooecia in the older portion (Text-fig. 4) are in the jumbled, semi-erect condition, with asexual and both kinds of sexual zooecia present. As in the recumbent part, marginal chambers are very well developed, and the attachment of the basal surface of the younger zooecia to the frontal surface of the older ones is well seen. There is, moreover, in some places an appearance as if the zooecia and incipient zooecia were budded from the chambers (c.f. the relation of the zooecia of *R. doliaris* to the kenozooecia), but special study is required to ascertain whether this is so and what is the real nature of the chambers.

The difference in the form of the zoarium as a whole in *Hippothoa hyalina* and *Reginella doliaris* presumably depends on the fact that the primary growth of *H. hyalina* is an ordinary recumbent crust and only the secondarily developed individuals are superimposed on their neighbours ; whereas in *R. doliaris* it appears that the first formed zooecia (ancestrula not recognized) are erect and all the zooecia are budded in the one manner and applied to erect predecessors.

GENERIC POSITION : *R. doliaris* resembles the type-species of *Reginella* in the characters of its frontal shield and flattened spines, and in having septula. *Cribrilina* Gray, type-species *C. punctata* (Hassall), has much in common with *Reginella* (see Osburn, 1950 : 174 (key) and 177), but possesses pore-chambers (dietellae).

Lumen-pores are not visible in the strongly calcified costae of *R. doliaris*, but they may be inconspicuous, and are sometimes not visible, in dry material of *R. furcata*, although they show well in transparent preparations of that species.

The erect position of the zooecia is probably not an important distinction between *R. doliaris* and typical *Reginella*, for the gradation from recumbent to erect zooecia is known in various genera, for example, *Beania* (see Hastings, 1943 : 408 (key), 413, c.f. *B. hirtissima* and *B. fragilis*).

Ovicells have not been seen in *R. doliaris*, and it differs from *R. furcata* in the conical form of the colony, and in the part played in its construction by heterozooecia (both kenozooecia and avicularia).

As already mentioned, avicularia are absent in the type-species of *Reginella*. Those of *R. doliaris* differ from those of *R.* (*Metracolposa*) *robusta* (see Canu & Bassler, 1917 : 35 ; 1920, pl. 40, fig. 2) in not having a complete cross-bar (pivot). In this feature *R. doliaris* resembles *Cribrilina*.

According to Jullien's description *Cribrilina alcicornis* Jullien (1883 : 508, pl. 14, figs. 23–25 ; Calvet 1907 : 399), a deep-water species from the Atlantic, off Spain, agrees with *R. furcata* in the characters of its frontal shield, and in having four flattened oral spines and a keeled hyperstomial ovicell.

In some respects *R. alcicornis* is intermediate between *R. doliaris* and more typical *Reginella* species. The " grandes ponctuations " in the interzooecial grooves appear to be kenozooecia comparable to those of *R. doliaris ;* and the avicularia are placed in the interzooecial grooves on each side of the orifice, and are without a cross-bar ; both points of resemblance to *R. doliaris.* The zoarium is, however, encrusting.

It is possible that the peculiarities of the colony of *R. doliaris* are of generic value, but it seems undesirable to introduce a new genus on the basis of a single colony without ovicells, especially as the zooecia suggest a close relationship to *Reginella.*[1]

Another possibility is that *R. doliaris* and *R. alcicornis* should both be separated from *Reginella* on account of their kenozooecia, since there is no evidence that these are present in typical species of *Reginella.* Structures which appear to be kenozooecia are widely distributed in the Cribrimorpha, and their taxonomic significance is uncertain. Waters (1923 : 559) mentioned " zooeciules ", " closed zooecia ", " blind zooecia " and " accessory cellules ", to which should probably be added " kenozooecia " (Canu, 1910 : 846–847), " interoecial tissue " (Lang, 1916 : 82), and " interzooecial tissue with chambers " (Waters, 1923 : 566–567). A few of these structures, although closed, have the cribriform wall, and are certainly equivalent to zooecia. In most, if not all, of the others their kenozooecial nature may be inferred. The part played by them in the building of the colony is various.

Membraniporella agassizii Smitt (1873 : 11, pl. 5, figs. 103–106) is a particularly interesting example. I have not seen a specimen of this deep-water species, which has not been rediscovered[2] (Osburn, 1940 : 404, and verbal communications from Dr. A. H. Cheetham and Dr. R. Lagaaij). However, Smitt gave a full description and excellent figures. The young zooecia have the characters of a typical *Membraniporella* except that they build an erect, branching, quadriserial colony. Gradually a profuse growth of kenozooecia and small avicularia envelopes these zooecia, appearing first in the interzooecial grooves, then spreading over the gymnocyst and finally covering the frontal shield. These older parts of the colony could be taken, superficially, for an ascophoran with a massive, thickened wall. (Have we here a hint (c.f. Smitt, p. 10) of how a pleurocyst may have evolved?) See Addendum.

In view of the evidence of a widespread tendency to the development of kenozooecia in various types of Cribrimorpha, I do not regard their development in *R. alcicornis* and *R. doliaris* as necessarily of generic importance. Conclusions drawn without seeing any specimen of the one species, and from a single specimen without ovicells of the other must be tentative, but, taking all the factors mentioned into consideration, I refer both species to *Reginella.*

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[1] On a visit to this country in 1955 Professor D. A. Brown read the script of this paper, and told me that he had recently completed a paper in which he had independently referred *Cribrilina alcicornis* and *Cellepora doliaris* to *Reginella* (see Brown, 1958 : 53).

[2] This is probably because subsequent collecting has mostly been in shallower water. Dr. Lagaaij (*in litt.*) has pointed out that Smitt's material came from 450 fms., at one of his two deepest stations (see Pourtalès, 1871 : 3), and that the numerous samples of Polyzoa from the Gulf of Mexico and Straits of Florida which he himself has examined included few from deep-water and only one from below 400 fms.

5. COMPARISON OF *REGINELLA DOLIARIS* AND *CONESCHARELLINA*

The differences between *R. doliaris* and the Conescharellinidae are such as to place them in different major groups, but they show zoarial resemblances in which they appear to afford an interesting example of convergence.

R. doliaris resembles the Conescharellinidae in the orientation of its orifices, the hinge of the operculum being on the side towards the periphery of the colony. In the Conescharellinidae the orientation of the zooecium and the homologies of its walls are matters for deduction and discussion.[1] In *R. doliaris* they are settled beyond question by the clearly recognizable cribrimorph frontal walls, which show that the orifice is in the normal position in relation to the frontal wall. Further comparison of the two is thus of special interest.

R. doliaris resembles *Conescharellina* in its more or less conical colony, built, with a profusion of avicularia and kenozooecia, by means of budding of new zooecia in the angles between existing ones.

The resemblance between the genus *Conescharellina* and *R. doliaris* goes even further. Silén (p. 20) has described the row of pores along the lateral wall of the zooecium and the lateral budding of *Conescharellina*, *Flabellopora*[2] and *Crucescharellina*. These pores (which may perhaps be small pore-chambers) are comparable to the lateral kenozooecia of *R. doliaris* in their position in relation to the zooecia, to the colony as a whole, and to the distal avicularia ; and the buds appear to arise similarly, except that in *Conescharellina* there is usually a regularity in the budding sequence which produces a geometrically exact arrangement of zooecia not found in *R. doliaris*.

The photograph of *C. breviconica* (pl. 1, fig. 4) illustrates some of these points. For purposes of comparison I shall assume that the orientation of the zooecia is the same as in *R. doliaris*, and call the zooecial wall at the growing edge of the cone the " frontal wall ". The line of pores belonging to an incomplete zooecium can be seen to be applied to the frontal wall of an underlying zooecium and aligned with an avicularium at the convex surface of the colony, just as the line of kenozooecia in *R. doliaris* is applied to the frontal wall of a zooecium and aligned with a surface avicularium (pl. 3, fig. 1).

It thus seems possible that the budding of the Conescharellinidae (whether from one or both series of pores) may be closely comparable to that of *R. doliaris*, and their structure to be interpreted in the same way. Whether this is ultimately confirmed or not, *R. doliaris* is of interest and importance because it shows that it is possible for the apparently inverted arrangement to arise without the major changes in the proportions and relations of parts of the zooecia that have been postulated in attempts to interpret the Conescharellinid colony.

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[1] See particularly Silén (1947 : 18) and Harmer (1957 : 722). Bassler (1953 : G230) adopted Silén's interpretation. Earlier Canu & Bassler (1929 : 498) regarded the zooecia of *Conescharellina* and *Flabellopora* as being orientated in the same way as those of *Reginella doliaris* now prove to be, and stated (legend to text-fig. 208C) that the " anatomical arrangements are the same as in other Cheilostomes ". But, because the orifice is in a plane at an angle to that of the supposed frontal wall, they regarded it as on the distal wall. Such a difference in plane between the orifice and the rest of the frontal wall can, however, be seen in normally orientated erect zooecia of many other Polyzoa (e.g. various *Cellepora* spp.) and does not call for special interpretation.

[2] Harmer (1957 : 753) gave an interesting description of the very curious colony of *Flabellopora irregularis* Canu & Bassler, in which the orifices of alternate series of zooecia open on opposite surfaces of the colony. There is one point which may usefully be added to his account, namely, that the proximal ends of the zooecia are separated from the surface of the colony by the heterozooecia (probably kenozooecia as well as avicularia) which form the irregular crust surrounding the adjacent orifices, shown in Harmer's pl. 49, figs. 2, 4.

6. ACKNOWLEDGMENTS

I should like to thank my husband, Dr. H. Dighton Thomas, who has read the script of this paper, and has given valuable counsel and encouragement ; Miss Elizabeth Pope for examining the part of the holotype of *Neoeuthyris woosteri* in the Australian Museum ; Mr. R. Ross for advice on botanical nomenclature and information about the alga associated with *N. woosteri*, and for making available specimens in the Botanical Department of the Museum ; Professor D. A. Brown, Dr. M. Burton and Dr. H. W. Parker who have all read the manuscript or parts of it and have discussed the nomenclatorial problems of *Lichenella brentii ;* Professor J. H. Day for the specimens of *Hippothoa* ; Professor T. Y. H. Ma for the material of *Crassimarginatella* ; the Keeper of the Manchester Museum for lending specimens from the Waters Collection ; Miss P. L. Cook for much reliable assistance and particularly for the compilation of the list of references and for two drawings ; and Mr. M. G. Sawyers for the photographs.

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8. ADDENDA

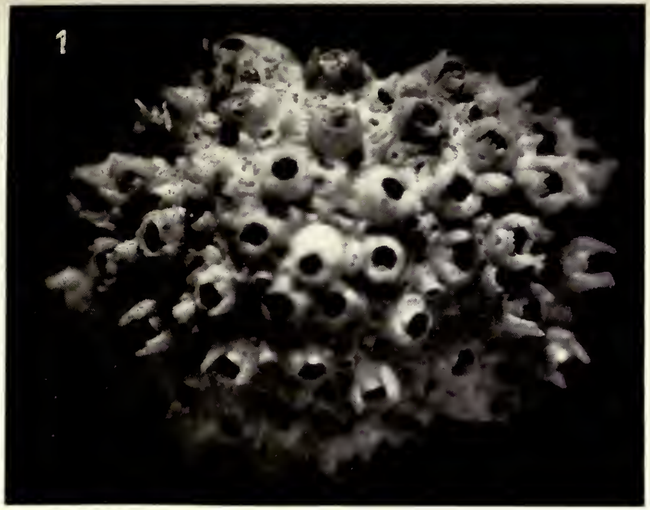
1. I have now examined Smitt's figured specimen of *Membraniporella agassizii*, see p. 258 above, and confirmed his account and figures. I am grateful to Dr. A. Andersson of the Riksmuseum, Stockholm, for lending the specimen.

2. Bobin & Prenant (1963, *Cah. Biol. mar.* 4: 40 *et. seq.*) have studied living ovicells of a species of *Bugula* with the calcareous parts shallow, see p. 250 above.

PLATE 1

Reginella doliaris (Maplestone) and *Conescharellina breviconica* Canu & Bassler

1. *Reginella doliaris.* 1909.11.12.14. Convex surface of colony focussed to show the periphery. × 20.
2. The same, photographed to show the central (apical) part. × 20.
3. The same colony, concave surface. × 20.
4. *Conescharellina breviconica.* 1931.12.30.175 (Canu & Bassler Coll.). Concave surface. × 20.



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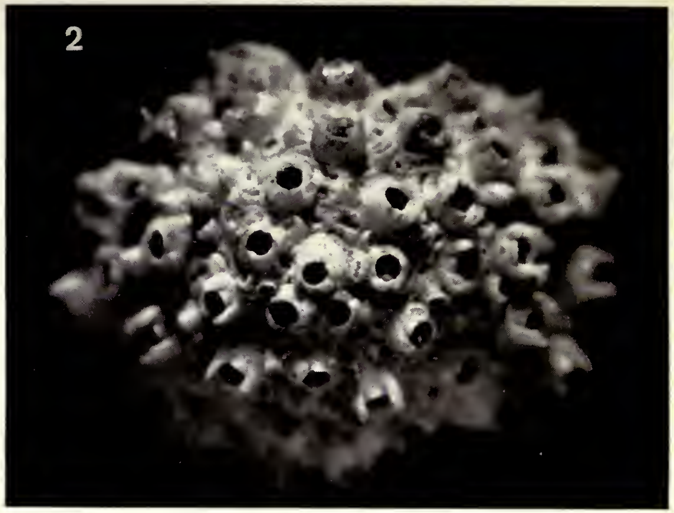

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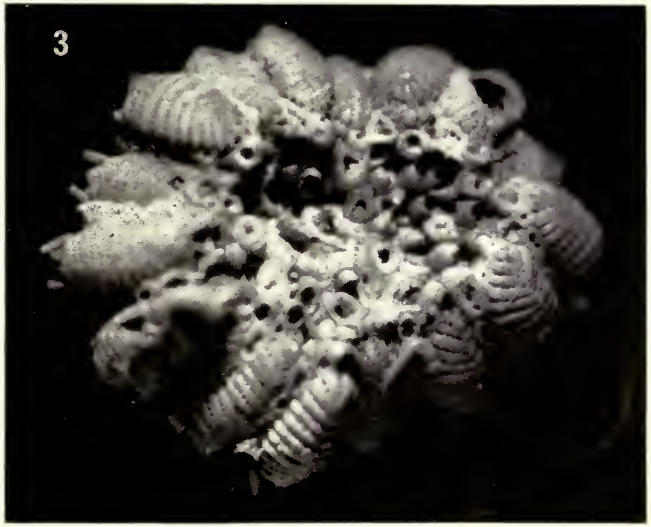

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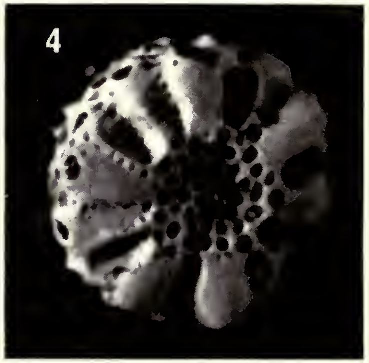

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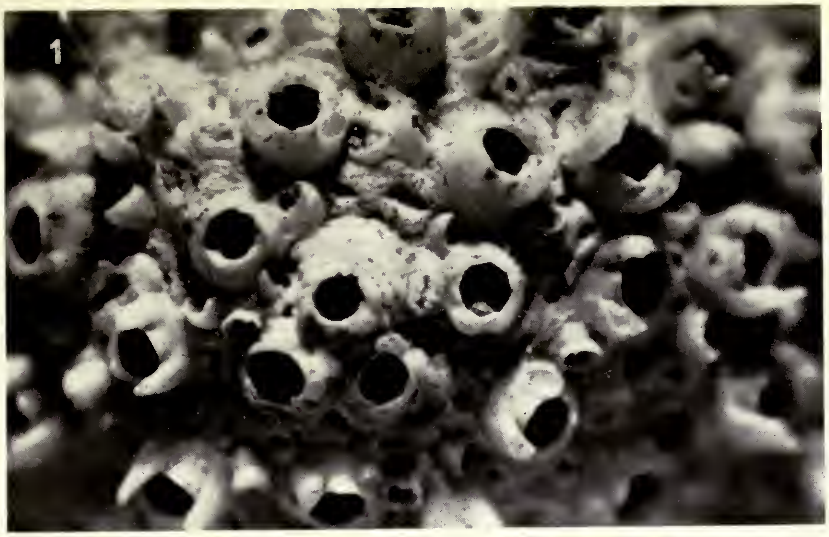
PLATE 2

Reginella doliaris (Maplestone)

1. Part of fig. 2 (pl. 1) enlarged, showing apical zooecia, with exposed cribriform wall ; interzooecial kenozooecia and avicularia ; and spines in various stages of abrasion. × 40.

2. Part of fig. 1. (pl. 1) enlarged, showing peripheral zooecia with unworn spines and distal plate. Note denticulate border of plate, and pit in its outer surface. × 40.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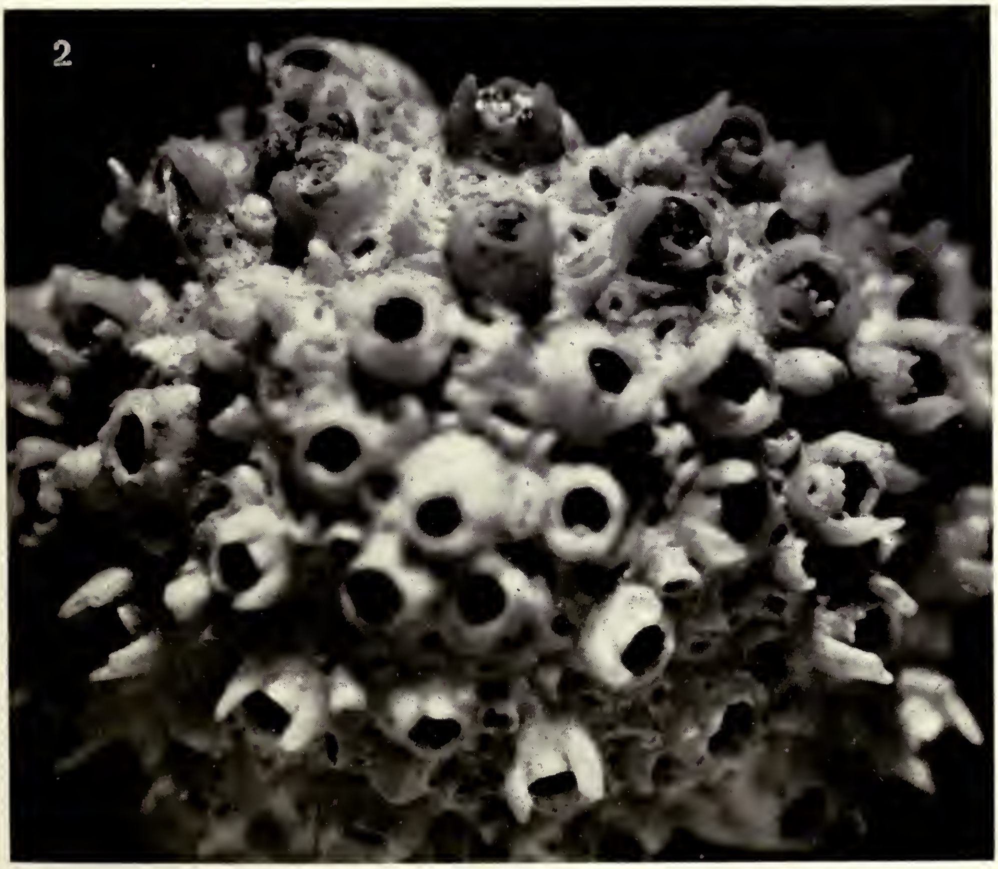
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PLATE 3

Reginella doliaris (Maplestone)

1, 2. Peripheral zooecia showing position of younger zooecia in relation to underlying older ones ; lines of interzooecial kenozooecia ; distal and proximal avicularia (at convex and concave surfaces of colony respectively) in series with kenozooecia. × 30.

3. Peripheral zooecia, frontal view, showing lateral spines and mucro on apertural bar. × 40.

4. Proximal end of a peripheral zooecium enlarged from fig. 5, showing proximal costae ; two septula (in middle of photograph) ; and adjacent kenozooecia and avicularia. × 60.

5. Part of concave surface of colony showing incipient zooecium applied to proximal ends of cribriform walls of two peripheral zooecia. × 40.

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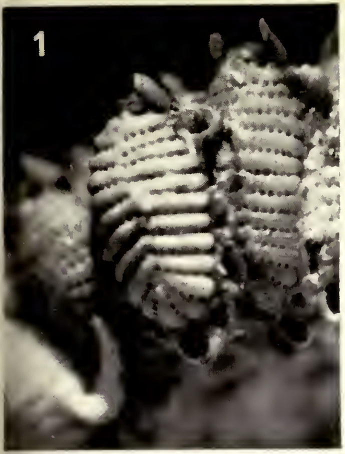

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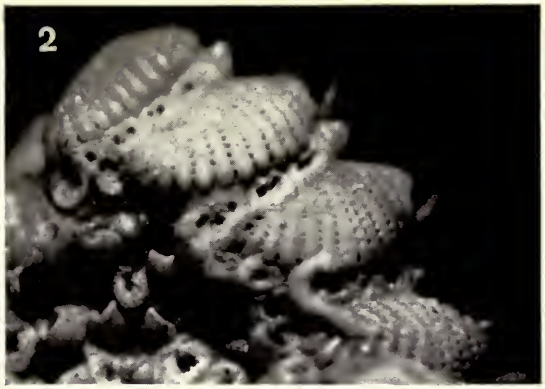

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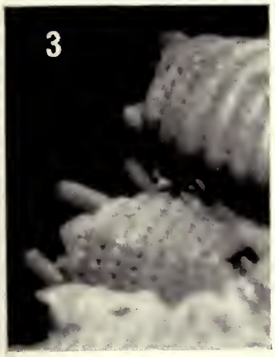

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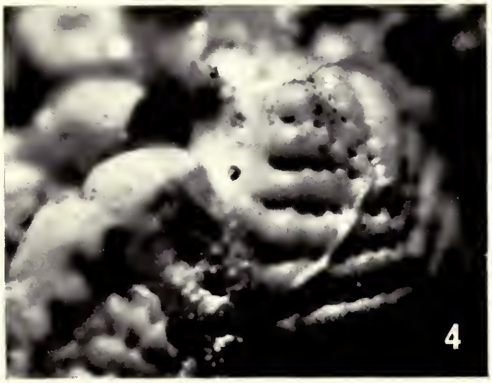

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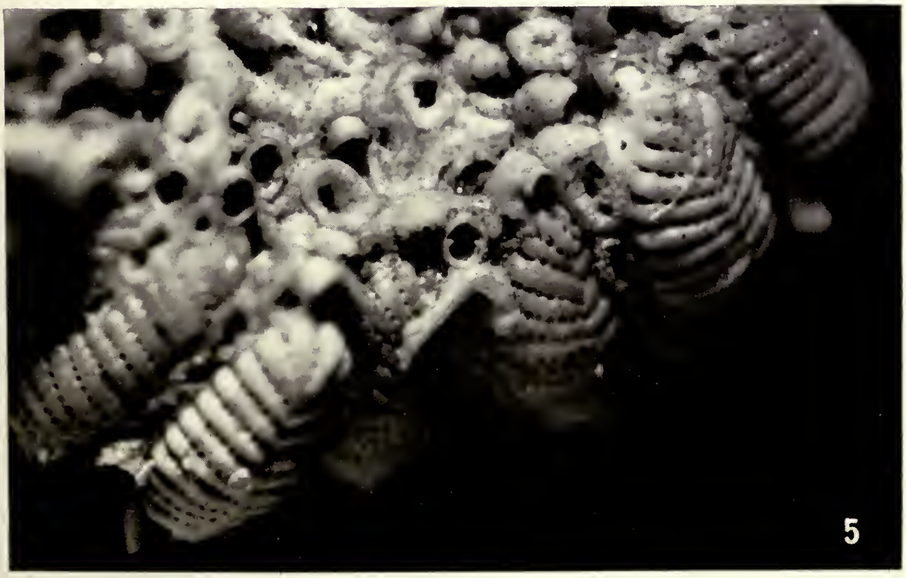

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25 FEB 1964

THE MARINE ENOPLIDA (NEMATODA): A COMPARATIVE STUDY OF THE HEAD

WILLIAM G. INGLIS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 11 No. 4
LONDON: 1964

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WILLIAM G. INGLIS
British Museum (Natural History)

Pp. 263–376 ; 194 *Text-figures*

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THE MARINE ENOPLIDA (NEMATODA): A COMPARATIVE STUDY OF THE HEAD

By WILLIAM G. INGLIS

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SYNOPSIS

This report is based on a collection of free-living marine nematodes from South African waters and is in two parts. The first part deals with the comparative anatomy of the head in the marine Enoplida and the second presents some comments on the classification of this group with the description of twenty-four species, of which twenty-two are named as new, belonging to eighteen genera, of which four are new. The species and genera treated are listed on page 300. The presence of a zone of fusion between the oesophagus and the body wall is characteristic of the families Phanodermatidae, Enoplidae and Leptosomatidae and it is argued that this is primitive and represents one of the major reasons for the evolutionary success of this Order of nematodes. The more specialized head forms in the same families are characterized by the presence of a fluid filled space at the anterior end of the body, the cephalic vesicle, the functional significance of which is discussed. It is the development of this vesicle which explains the appearance of many of the characteristic structures of the head. Thus, in the Phanodermatidae the presence of six rods in the lining of the buccal cavity appears to be common and they occur in *Phanoderma*, *Dayellus* gen. nov. and—what can be interpreted as homologues—in *Crenopharynx*. These rods and the mandibles in the Enoplidae always lie in close relationship to the nerves which supply the labial sense organs and it is argued that they have arisen as supporting structures. In the Enoplidae it is shown that the head structures represent components in a functionally interrelated complex and that mandibles of forms such as *Enoplus* represent the fusion and condensation of an elaborate system of diverse structures. The " mandibles " arise from two sources, one anterior to the oesophagus, the buccal cavity, and one in the anterior end of the oesophagus itself, the onchial cavity. The buccal cavity component represents three structures, a median plate of thickened cuticle and two flanking rods—which are probably homologous with the buccal rods of the Phanodermatidae. The onchial cavity component represents a plate of thickened cuticle developed in association with the three large onchia characteristic of many groups of this family and it is on to this plate that all the specialized musculature at the anterior end of the oesophagus is inserted. No musculature is inserted on the mandibular—or buccal cavity—component. The structures derived from these two sources in some cases fuse, as in *Mesacanthion*, but the original components can still generally be made out. The onchial plate is extended as narrow arms towards the radii of the oesophagus and the onchial: mandibular complex is slung by these arms so that it can rotate around a line lying between two rings of specialized anterior oesophageal musculature. This musculature is so arranged that contraction of the anterior ring causes the mandibles to open and contraction of the posterior ring acts in apposition. In the Leptosomatidae the head is characterized by the oesophageal musculature passing anteriorly through the cephalic vesicle so that the buccal cavity is always small and no structures develop in the wall of the buccal cavity to support the sense organs. Structures comparable to buccal rods, but probably of little evolutionary importance, are developed on the anterior edge of the cephalic capsule in forms such as *Parabarbonema* and *Thoracostoma*. In the Oncholaimidae no trace of the cephalic vesicle can be found but in *Pontonema*, at least, the remains of a cephalic capsule are present and it is argued that the large mouth capsule in this family is an enlarged onchial cavity and that the buccal cavity has been lost or almost completely suppressed. It is suggested that the Phanodermatidae, Enoplidae and Oncholaimidae represent a group of related forms separate from the Leptosomatidae and possibly the Oxystomidae and Ironidae, which probably represent another group of related forms. The Eurystominae and Enchilidiinae probably arose from the first line but are almost certainly not themselves closely related. From this it follows that in the first group of families there has been a series of evolutionary changes from mouth openings bounded by three lip-lobes to those with six lip-lobes then to three large lips and finally six lobes again or even no lip-like structures at all. The argument is advanced that to attempt to derive the various forms of the mouth structures in the Nematoda as a whole from one simple form is a mistake since they appear to represent the expression of independently acquired structures developed from an extremely labile region. Thus the term lip has only descriptive significance and can carry no indication of homology. It has been necessary to introduce a number of morphological terms and these are listed, with definitions, on page 296. Among the taxonomic observations made the following are worthy of special note : *Thoracostomopsis* Ditlevsen, 1919, is a typical member of the Enoplidae and the so-called spear in the mouth is composed of three long, thin wholly cuticular onchia. The present classification of the families Enoplidae and Leptosomatidae is most unsatisfactory as there are probably several evolutionary lines classified horizontally within them. In particular the delimitation of the genera *Enoplolaimus*, *Mesacanthion* and *Enoploides* is unsatisfactory. Because of the difficulty involved in studying this satisfactorily no changes have been proposed in the classification but attention is drawn to the apparent weaknesses. The Superfamily Tripyloidea is not accepted but, because almost all the criticism offered is destructive, it is suggested that the classification of the Order used by Wieser (1953), that is to families only, should continue in use.

INTRODUCTION

The marine representatives of the Nematode Order Enoplida were first adequately treated by Filipjev (1916) and later (1927) in " Les Nématodes libres des mers septentrionales appartenant à la famille des Enoplidae " the foundation of what is now treated as at least a Suborder was laid down. Filipjev (1934) presented the first reasonable classification of the Nematoda as a whole, a classification which Chitwood later (1933, 1937, 1937a and 1950) modified. This modified version has been accepted for some time although there have been various criticisms of it, notably that of Hyman (1951). However, it has become increasingly clear that the Chitwood classification is unsatisfactory until Chitwood (1960) can say " . . . the classification of the Nematoda is at present in no condition to be stabilized . . . " and later he (1962) and Goodey (1963) have, rightly, accepted that his division of the Nematoda into two major groups can no longer be accepted. Comments on the classification of the marine Enoplida have been made at various times by a variety of authors, De Coninck, Gerlach, Schuurmans Stekhoven and Wieser in particular. Most recently Clark (1961) has published a " Revised classification of the Order Enoplida ". which he modified slightly later (1962). In spite of the passage of more than thirty-five years Filipjev's 1927 classification of the marine Enoplida has remained essentially unaltered although most of his subfamilies are now treated as families. Thus the Superfamily Enoploidea of Clark contains the same groups as were included in the family Enoplidae by Filipjev, with the addition of a few groups discovered since Filipjev's publication. Further, Filipjev, most clearly in 1934, separated the Enoplidae as containing those forms with " Cuticle with duplication on the head " and this character is used by Chitwood (1950) and by Clark (1961) in delimiting the Superfamily Enoploidea. In spite of the classification of the marine Enoplida being based largely on the structure of the head it has never been adequately analyzed. Even Wieser's (1954) treatment of the Leptosomatidae is incomplete. Such an analysis is an urgent requirement and, although I have previously been able to make some isolated observations on the structure of the head in some genera of the Enoplida (*Trissonchulus* (Inglis, 1961), *Enoplus*, *Phanoderma*, *Oncholaimus*, *Prooncholaimus*, *Symplocostoma* and *Eurystomina* (Inglis, 1962) I had been unable to study any wide range of head structure when Professor J. H. Day, University of Cape Town, Republic of South Africa asked me to look at the free-living marine nematodes collected by the Ecological Survey of the

Department of Oceanography of that University. As a result of studying these specimens I have been able to work out the structure of the anterior end in a wide number of different forms, particularly forms with so-called mandibles (i.e. Enoplidae sensu Wieser) and am able to describe the comparative morphology of the head and to discuss the functional demands which have, to some extent at least, determined it. The most immediate result is to complicate the taxonomy : almost certainly because of insufficient information about the groups under consideration.

This report is in two parts. The first part deals with the structure of the head, particularly in the family Enoplidae—this is a result of basing the study on a general collection and simply represents the dominance of this family in the samples—and the second gives descriptions of the species studied with some observations on the classification of the marine Enoplida.

THE STRUCTURE OF THE HEAD IN THE MARINE ENOPLIDA

INTRODUCTION

The most immediate, and long standing, errors in the interpretation of the structure of the head in the marine Enoplida are the misunderstanding of the so-called "doubled cuticle" and the reference to the mandibles of the Enoplidae as consisting, in many forms, of pillars connected anteriorly by bars. The "doubled or duplicate cuticle" of the head is the result of the presence of a fluid filled space at the anterior end of the body, which I propose to call the *Cephalic ventricle*, the origin of which has been misunderstood by Filipjev. The only attempt to describe this structure is that of Filipjev (see Filipjev and Schuurmans Stekhoven (1941)) where he shows the outer cuticle of body curling in to the mouth opening and running backwards to rejoin itself posterior to the anterior end of the oesophagus, thus forming a pocket at the anterior end of the body. This interpretation is not correct, as I shall show. Filipjev (1927) considered the short mandibles and lack of onchia in *Enoplus* to be primitive while Chitwood (1950) appears to suggest that this condition is not primitive, an opinion which Wieser (1953) advances unequivocably. The mandibles appear to have been dismissed by all previous workers as relatively simple wholly homologous structures. Thus Wieser (1953 and 1959), for example, refers to rods or bars connected anteriorly by a curved bar and goes so far as to distinguish between two genera on the character that the mandibular pillars are rod-like in one and are plate like in the other (*Mesacanthion* and *Epacanthion*). In fact the mandibles are, in most cases, one curved mass of thickened, darkened cuticle developed in the cuticle lining the anterior end of the oesophagus and the buccal cavity. The apparent presence of rods, pillars, plates or similar elaborations is due in most cases to studying the incurved ends of these plates of dense cuticle in optical section. Thus the descriptions simply refer to the thickness of the modified cuticle making up the mandibles.

GENERAL MORPHOLOGY OF THE HEAD

It is essential to consider the head as a unit. To consider only one part in isolation must, inevitably, lead to error. Further, in all the other groups which I have studied it has been possible to show that the structure of the head—that is the form of the mouth opening and bounding lips or lip-like structures, the shape of the buccal cavity and the modification of the anterior end of the oesophagus—forms a functional whole and must be analyzed as such (Inglis, 1958, 1960 ; Inglis & Diaz-Ungria, 1960). This is equally true in this group of nematodes. The most significant and probably the most immediate factor in determining the form of the head in the Enoplida is the way in which the oesophagus is attached to the outer body wall or the cuticle of the body. To this simple yet effective modification may be attributed part of the success of the Enoplida. This success is amply witnessed by the large size and numbers of the members of the group and their widespread occurrence in marine, fresh-water and soil habitats and as parasites. Their success is not wholly to be attributed to this since the appearance of spiral fibres within the cuticle must also have played a large part in their evolutionary advance (see Inglis, 1964). In fact the structure of the cuticle supplies one of the most conservative characters of the entire Order. Associated with the attachment of the oesophagus to the body wall over a large area at its anterior end is the modification of the inner layer(s) of the body cuticle to produce the spectacular *cephalic capsule* so characteristic of forms such as *Thoracostoma*. But the most unexpected result of the present study has been the realization that the mandibles of the Enoplidae are very closely associated with the distribution of the nerves which supply the inner circle of cephalic sense organs and that their functional origin must have been that of supporting structures, a function which they still clearly fulfil even in highly modified groups.

The head types fall into two major structural groups, one in which the oesophagus is attached at its anterior end to the outer body wall and a second in which there is no such attachment, or at least such an attachment is not obvious. The first group is frequently characterized by the presence of a dense component derived from the inner layers of the cuticle (endo- and meso-cuticle ; see Inglis, 1964) at the anterior end of the body, the *cephalic capsule*. In many genera this is the only obvious modification of the head. It frequently corresponds to the zone of attachment of the oesophagus to the body wall but not always and not wholly. It also tends to be more obvious in forms with well developed buccal armature (e.g. *Thoracostoma*). The cephalic capsule is frequently divided into lobes posteriorly by a series of *incisions* (see Wieser, 1954) of which, when they are present, there are always six, two lateral, two dorso-lateral and two ventro-lateral. Such incisions are always present when the cephalic sense organs lie anterior to the posterior edge of the cephalic capsule and represent the external expression of the internal foramina–between the body wall and the oesophagus–through which the nerves pass. The capsule is frequently roughly punctate and this appears to be a reflection of the fusion of the oesophagus to the body cuticle since such markings do not occur over the incisions. In most cases the incisions expand anteriorly to form roughly circular areas from which the cephalic setae arise. These are called *fenestrae*. In some cases the external covering of the anterior end of the oesophagus becomes thick and dense to form a second capsule, which I shall call the *oesophageal capsule* (see Text-fig. 1). This is what Wieser (1954) calls the pharyngeal capsule but at that time he was calling the oesophagus the pharynx. This is technically correct, as Hyman (1951) points out, but the term oesophagus is so firmly embedded in nematode literature that to attempt to extract it would only lead to complications with no compensating advantages. Wieser (1954) proposes the term " stomadaeal capsule " for two subsiduary capsules—the oesophageal capsule and the " Buccal capsule " (my terminology) which he considers to be " . . . built up of the walls of the vestibulum, buccal cavity and the anterior pharyngeal lumen . . . ". I do not accept the term stomadaeal capsule as it covers structures which arise from too many and too diverse origins to be adequately covered by one term. Further, the two sub-capsules proposed by Wieser are totally different in origin and function as I shall demonstrate below. The oesophagus is attached to the body wall in the region of the cephalic capsule at three zones in some forms, e.g. *Enoplus*, over most of the length of the capsule while in others the attachment is complete round the circumference of the oesophagus for most of the length of the cephalic capsule, e.g. *Enoplolaimus*. In all cases the union between the oesophagus and the body wall is complete at the anterior end of the oesophagus, with the minor exception of the foramina through which pass the nerves to the inner circle of or *labial sense organs*. At this point of complete fusion or the level at which the oesophagus terminates anteriorly the cephalic capsule is frequently thickened as a distinct ring, the

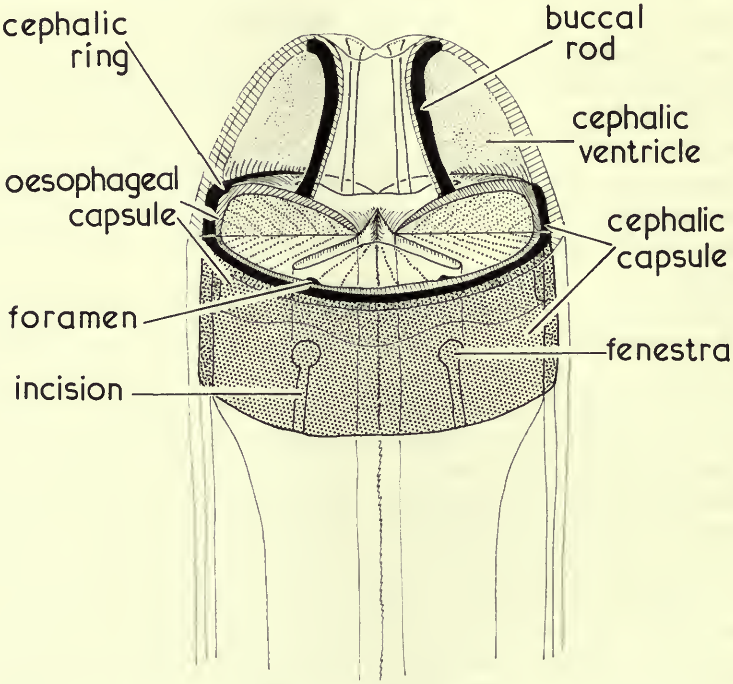

FIG. 1. Sectional view of a generalized Enoplida head from the dorsal surface.

cephalic ring. Wieser calls this structure the " stomadaeal ring " but its origin from the cephalic capsule is quite clear when the relationships to the nerves which supply the labial sense organs are studied. These nerves always pass beneath the cephalic ring, showing that the ring does not take its origin from the oesophagus (see Text-fig. 87). The oesophagus, in many of the elaborate forms, stops some distance posterior to the extreme anterior end of the body and it is in such forms that a prominent cephalic ring occurs. The remainder of the body anterior to the oesophagus is a fluid filled space (see Figs. 1 and 2) which is much reduced in some forms with complex cephalic armature, e.g. *Enoplus*, *Enoplolaimus* and *Thoracostoma*, but is prominent and obvious in forms such as *Dayellus* (Text-figs. 38 and 41). This is the space I propose to call the *cephalic ventricle* and it is this space which has led Filipjev to misinterpret the way in which the cuticle of the body is attached to the oesophagus. The occurrence and appearance of all these structures varies, for example the cephalic capsule extends anterior to the cephalic ring in some forms ; in others there is no cephalic vesicle, and various other structures also occur. This variation in the occurrence and form of the morphological structures will be treated in detail below, by families.

THE STRUCTURE OF THE HEAD IN THE PHANODERMATIDAE

I have previously reported the presence of six cuticular rods, in the genus *Phanoderma*, which are developed within the cuticular lining of the buccal cavity (Inglis, 1962) and have found them in another species of the same genus, *Phanoderma unica* (see page 309). The same structures are present in *Dayellus dayi* (see page 304) where they are much more easily seen as the anterior end of the oesophagus in this genus is simple (Text-figs. 38 and 41). These rods, which I propose to call *buccal rods*[1] (Text-fig. 1), are always closely associated with the nerves which supply the labial sense organs (Text-figs. 38, 39, 41, 50, 53 and 54), (I shall use the term *buccal cavity* to mean the lumen of the digestive tract from the anterior end of the oesophageal lumen to the exterior.). In *Dayellus* the cephalic and oesophageal capsules are fairly well developed, the cephalic ventricle is very prominent and the anterior end of the oesophagus is simple without armature of any kind. That is, there are no onchia, plates or other elaborations of any kind (Text-figs. 38 and 41). The mouth opening is bounded by six lobes and there are no flaps by which it can be closed (Text-fig. 39). The genus *Phanoderma* is as described before (Inglis, 1962) with well developed cephalic and oesophageal capsules, two massive cuticular *onchia* ventrally and one small *onchium* dorsally (*Onchium* is a name proposed by Cobb (1919) for tooth-like structures which arise from the oesophagus and *odontium* applies to similar structures arising from the lining of the buccal cavity). Six buccal rods are present and the mouth opening is bounded by six lip-lobes as in *Dayellus*. A cephalic ventricle is present but is reduced relative to the condition in *Dayellus* (Text-figs. 50, 53 and 54. Figs. 7–9 and 12–13 in Inglis, 1962). It should be noted that in *Phanoderma* the onchia project freely into the buccal cavity and are not embedded in the walls of that cavity. In some species of *Phanoderma* the body cuticle posterior to the cephalic capsule is marked by longitudinal striations which form the so-called *cervical capsule*. Such a capsule is not present in *P. unica* but is present in, for example, *P. parafilipjevi* which I redescribed in 1962.

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[1] Definitions of all the morphological terms proposed or employed are given on p. 296.

Two species of the genus *Crenopharynx* are described later (pages 306 and 308) and the structure of the head is the same in both. The cephalic capsule is lightly built and there does not appear to be an oesophageal capsule. The cephalic ventricle is slight and no buccal rods appear to be present when the head is studied in any view other than *en face* (Text-figs. 43 and 49). The anterior end of the oesophagus is covered by fairly thick cuticle (?incipient oesophageal capsule) and projects anteriorly as three lobes. These lobes appear to project freely into the buccal cavity and do not lie embedded in the surrounding cuticle of the buccal cavity. I cannot, in view of the small size of the specimens, be sure but in *en face* preparations the cuticle covering the radial surfaces of the anterior lobes of the oesophagus appears to be in two layers, one from the oesophagus and one from the wall of the buccal cavity. The mouth opening is tri-lobed and in surface view, *en face*, the inner circle of sense organs appears to be supported by a series of buccal rods (Text-fig. 43). A more careful examination, however, shows that this effect is due to a thickening of the cuticle lining the buccal cavity. Because the oesophagus is developed anteriorly as three lobes each lobe projects between a pair of the nerves supplying the inner circle of sense organs. Also, each arm of the lumen of the oesophagus, or buccal cavity, lies between a pair of these nerves so that each nerve is separated from one neighbour by a lobe from the oesophagus and from the other neighbour by one of the radii of the buccal cavity. As a result each nerve, and as a corollary each labial papilla, is enclosed in a V-shaped cuticular structure one arm of which corresponds to one side of the radial lumen of the buccal cavity and the other arm of which corresponds to one side of a lobe of the oesophagus (see Text-figs. 43 and 44). This arrangement of the head and its contained structures reflects the mechanical necessity of fitting twelve structures into the circumference of the body, the three radii of the oesophageal/buccal cavity lumen, the three anterior lobes of the oesophagus and the six nerves to the labial sense organs. It will be argued later that this condition could represent the origins of the buccal rods occurring in forms such as *Phanoderma* and *Dayellus*.

Throughout this family the labial sense organs appear as papillae while the outer or *cephalic sense organs* are in the form of setae and always lie in one circle of ten of which six are longer than the remaining four. The extent to which the oesophagus fuses to the outer surface of the body is difficult to establish in view of the relatively small size of the head in all members of the family but it appears to take the form of three zones of attachment which widen anteriorly until the fusion is complete near the posterior end of the cephalic vesicle, when present. There are no marked modifications of the cephalic capsule in the form of incisions or fenestrae.

THE STRUCTURE OF THE HEAD IN THE ENOPLIDAE

The form of head characteristic of this family is the most complex in the entire Order and is the form which I have been able to study most thoroughly. Its structure will be considered under two headings, the skeletal component and the muscular. It should be noted that in this family, in particular, all the dense cuticular components are developed within the thickness of the cuticle, and, apparently, always in the deepest layer(s) (see Inglis (1964) for a detailed discussion). As a result the mandibles which are so prominent and so important taxonomically lie within the sheets of cuticle forming the walls of the buccal cavity and simply represent specializations of these sheets and not independent organ systems. The labial sense organs take the form of an inner circle of setae in all the genera, except *Enoplus*, and the cephalic sense organs occur in roughly one circle of setae of which six are longer than the remaining four. In many cases, however, this arrangement becomes more condensed so that each of the four short setae lies immediately posterior to the dorso- and ventro-lateral representatives of the six long setae (see Text-figs. 29, 30, 55, 59, 60, 62, 74, 76, 86, 87, 91, 98, 104 and 109). In addition to the setae there are the usual lateral amphids, which are generally small and lie about the posterior edge of the cephalic capsule, and a pair of sense organs which are latero-ventral in position between the two circles of sense organs. These *cephalic slits* appear to be universal among the members of the Enoplidae and show marked variation from genus to genus. They are small in some, such as *Enoplus*, and very large in others, e.g. *Mesacanthion* (Text-figs. 77, 79 and 85) and *Trileptium* (Text-figs. 99 and 100), but in all such cases the organ consists of a small opening to the exterior which leads in to a chamber of varying size from the base of which a nerve runs posteriorly and the difference in the appearance from species to species is determined almost wholly by the size and shape of this chamber. In a few cases the cephalic slit is modified to form what Wieser (1953) has called a *cirrus*. This is a long anteriorly projecting club-shaped organ which arises from the same position as that generally occupied by the cephalic slit and is clearly a modification of that organ. Wieser (1953) reports it from three species, *Oxyonchus dentatus* Ditelvsen, 1919, *Parasaveljevia lupata* Wieser, 1953 and *P. cirrifera* Wieser, 1953. Later (1959) from *Oxyonchus culcitatus* Wieser, 1959, he reports a well-developed cirrus in the same region of the head and in an *Oxyonchus* species he describes a slight elevation. A well developed cirrus is present in *O. ditlevseni* (page 311, Text-fig. 57). As Filipjev (1927) suggests, in the case of the small elevations he has seen, these cirri are possibly due to the eversion of the pocket of the cephalic slit. The small inner pocket of the cephalic slit in *Enoplus* looks suspiciously like an introvert cirrus, or vice versa.

SKELETAL COMPONENT OF THE ENOPLIDAE HEAD

A cephalic capsule is always present and well developed and there are always three *mandibles* of varying shape and degrees of massiveness present, one corresponding to each sector of the oesophagus. A distinct cephalic ring is always present and the anterior end of the oesophagus is always covered by thick cuticle to form a simple oesophageal capsule which does not appear to extend posteriorly much beyond the level of the cephalic ring. Posterior to the cephalic capsule in several genera there is a zone covered by dot-like markings. This appears to be homologous with the cervical capsule of the Phanodermatidae. The cephalic ring persists round the entire circumference of the body (see Text-figs. 62, 76, 86 and 87) and tends to curve posteriorly in the inter-labial regions. The anterior surface of the oesophagus always slopes posteriorly from the level of the cephalic ring towards the interior of the body so that its attachment to the complex of internal cuticular structures is always at a level more posterior than its outer limit (Text-figs. 16, 17, 24, 34, 57, 60, 62, 70, 74, 80, 100, 104 and 110). The mouth opening is tri-radiate with three large lips which are separate for some distance posteriorly along the body.

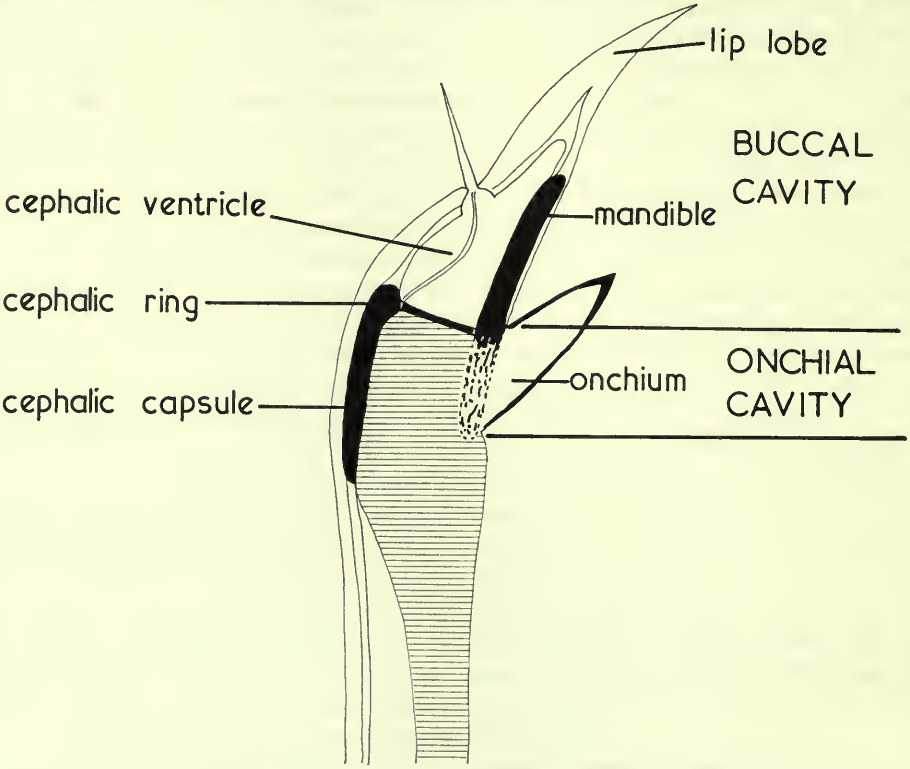


FIG. 2. Generalized longitudinal section through one lip of an Enoplidae head.

In effect the mouth opening is three dimensional in comparison to the terminal condition occurring in the Phanodermatidae which can be described as two-dimensional (see Inglis (1962) where I employ the same terms in the same way). The cuticle on the inner face of each lip is thickened over a specialized median zone to form the dense mandibles and the cephalic ventricle is subdivided by the posterior extension of the mouth opening to form three subsiduary pockets, one corresponding to each lip, each of which, in turn, corresponds to one sector of the oesophagus. The anterior limit of each ventricle is just anterior to the anterior edge of the corresponding mandible. Anterior to this line of fusion the lip is a solid sheet of cuticle which I shall call the *lip-lobe*. This lip-lobe thins evenly towards its rounded anterior edge which is developed in most cases into a small subsidiary lobe (Text-figs. 59, 60, 70, 85, 86 and 90). The lip-lobe is generally thickened on each edge along a zone corresponding to the edges of the mandibles (Text-figs. 85, 90, 93 and 95).

The most typical condition in this family is for the anterior end of the oesophagus to be cupped to form a cavity into which project three massive wholly cuticular onchia. Thus the entire mouth cavity is derived from two sources and is divided into two parts, one lying anterior to the anterior end of the oesophagus on a level corresponding with that of the cephalic vesicles and one lying posterior to the anterior limit of the oesophagus, which is wholly surrounded by oesophageal tissue or specializations of oesophageal origin, in which lie the onchia. The first of these chambers I shall call the *buccal cavity* and the second the *onchial cavity*. Thus, if a lip is considered in longitudinal section through its mid-line there are four points of reference, one—the point of fusion where the ventricle stops anteriorly, two—the anterior edge of the mandible, three—the anterior end of the oesophagus and four—the posterior end of the cephalic capsule (Fig. 2). The two cavities show some variation in shape. The onchia may be equal in size, as in *Enoploides* or *Mesacanthion*, or the dorsal may be much smaller than the two equal ventro-lateral as in *Oxyonchus* (Text-fig. 55). Except in some very exceptional genera, e.g. *Trileptium*, no other variation is shown by the onchia except for a gross variation in their size and their complete reduction in *Enoplus*. The cuticle lining the onchial cavity is always thickened but the degree of this thickening varies considerably. For example it is not marked in forms such as *Africanthion* (Text-figs. 91 and 95) but is very marked in forms such as *Mescanthion* (Text-figs. 84 and 89).

The mandibles are generally described as consisting of two lateral pillars with an anterior, curved connecting bar, except in a few special cases such as, for example, *Hyalocanthion* Wieser, 1959. This is incorrect, although a reasonable description of the appearance of the mandibles from a superficial examination. In all the forms I have studied the mandibles represent a solid thickening of the lining of the buccal cavity wall which curves with the shape of the body so that, when it is viewed from the outer aspect there appear to be two bars because the mandible is being studied in optical section. Thus Wieser's (1953) separation of the genera *Epacanthion* and *Mesacanthion* on the presence of rod-like or plate-like lateral pieces to the mandibles is based on a misunderstanding of the conditions present. This does not invalidate the use of such characters since it may still be valuable to use the thickness of the mandible in this way. When the inner surface of the lip is studied a distinctly striated semi-circular zone of cuticle is seen flanking the mandibles which I propose to call the *semi-lunar striations*. (Text-figs. 30, 36, 61, 72, 95 and 101). The more anterior limit of this striated area runs from the tip of the mandible and curves round to the inter-labial spaces and terminates along a posteriorly curved line posteriorly. This posterior limit lies at the level of the anterior edge of the oesophagus where it attaches to the onchial cavity. The mandibles project from the surface as two small points or processes at their extreme antero-lateral tips only (Text-figs. 61, 89 and 95). Posteriorly the mandibles narrow and then flare out again to form part of a transverse bar of dense cuticle which extends from one flanking inter-labial space to the other. It is along this bar that the semi-lunar striations stop posteriorly. Immediately posterior to this bar, which I propose to call the *mandibular ring*, is the line of attachment of the oesophageal tissues to the thickened cuticle lining the onchial cavity. The separation between the two cuticular masses at this level is shown clearly in forms such as *Enoploides* (Text-fig. 30) but in extreme cases, such as *Mesacanthion*, the mandibles become so closely associated with the cuticle of the onchial cavity—the *onchial plate* as I shall call it—that there appears to be only one structure present. Similarly in *Enoplus*, in particular, the fusion of the buccal and onchial components has been carried so far that there is only one functional and, apparently, morphological unit left. Nevertheless even here the division into an anterior and a posterior component can still be made out and over the entire family it is clear that the term mandible has been applied in different ways in different genera. In *Enoplus* the whole complex is what has been called the mandible while in *Enoploides*, for example, what have been called mandibles are really only the buccal component of the entire complex. This latter use of the term has, in general, been the more common and I therefore restrict its use here to that sense. The *mandibles*, therefore, represent a thick dense specialization of the median part of the cuticle lining the buccal cavity.

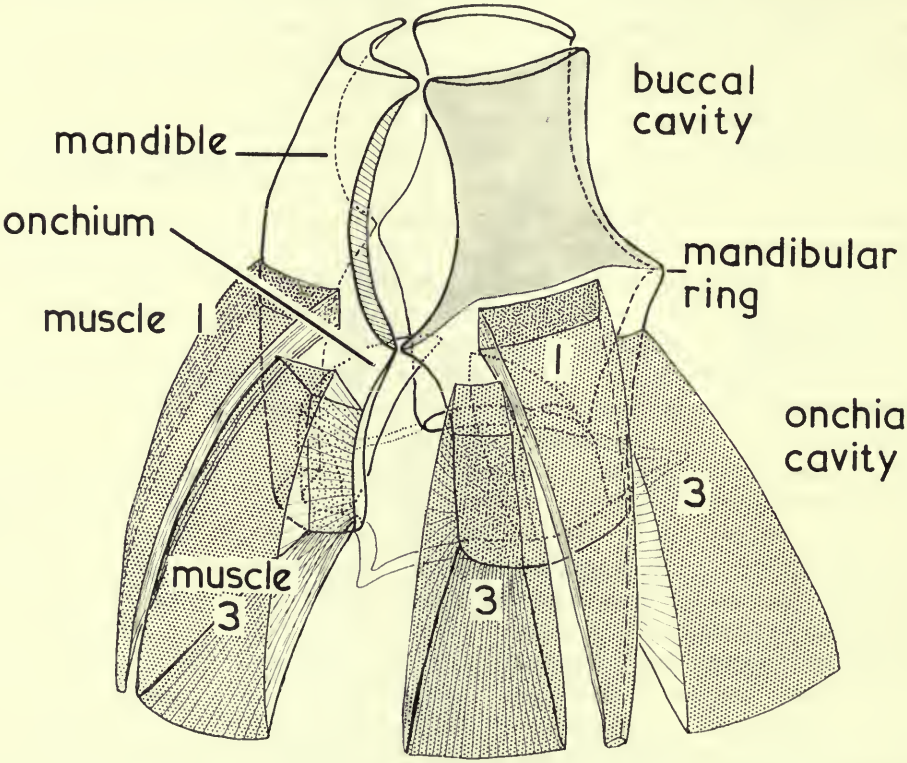


FIG. 3. The mandibular : onchial complex of a generalized Enoplidae head with simplified musculature.

In all cases the mandibles and the onchial plates form a functional unit which is broad antero-posteriorly in its middle region but narrows rapidly towards the edges of the lips—that is towards the inter-labial spaces—so that the onchial plate forms a massive central plate, which corresponds to each oesophageal sector, supported by two processes, the *radial processes* (Text-figs. 5–7) which extend laterally to meet at the outer ends of the oesophageal radii (Text-figs. 69, 83 and 87). It should be noted that the mouth opening is closed radially by external cuticle much further anteriorly than it is internally (Text-figs. 62, 76, 80 and 87). Internally the separation of the lips and the sectors of the onchial cavity continues to the level of the mandibular ring—which effectively forms the anterior limit of the onchial plate. The musculature at the anterior end of the oesophagus is highly specialized (see page 283) and from about the level of the posterior edge of the cephalic capsule forward the parts of the oesophagus opposite the outer ends of the radii of the oesophageal lumen become increasingly cuticularized. These zones of dense material lying within the oesophagus I shall call *radial masses* (Text-figs. 5, 6, 7, 25, 26, 29 and 80) and the onchial plates are attached to these masses by their radial

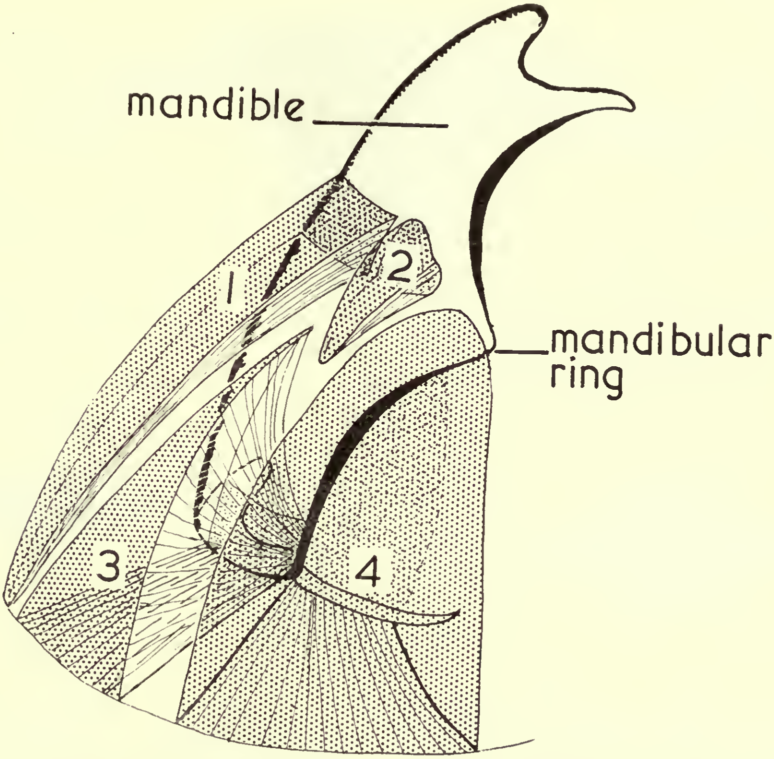
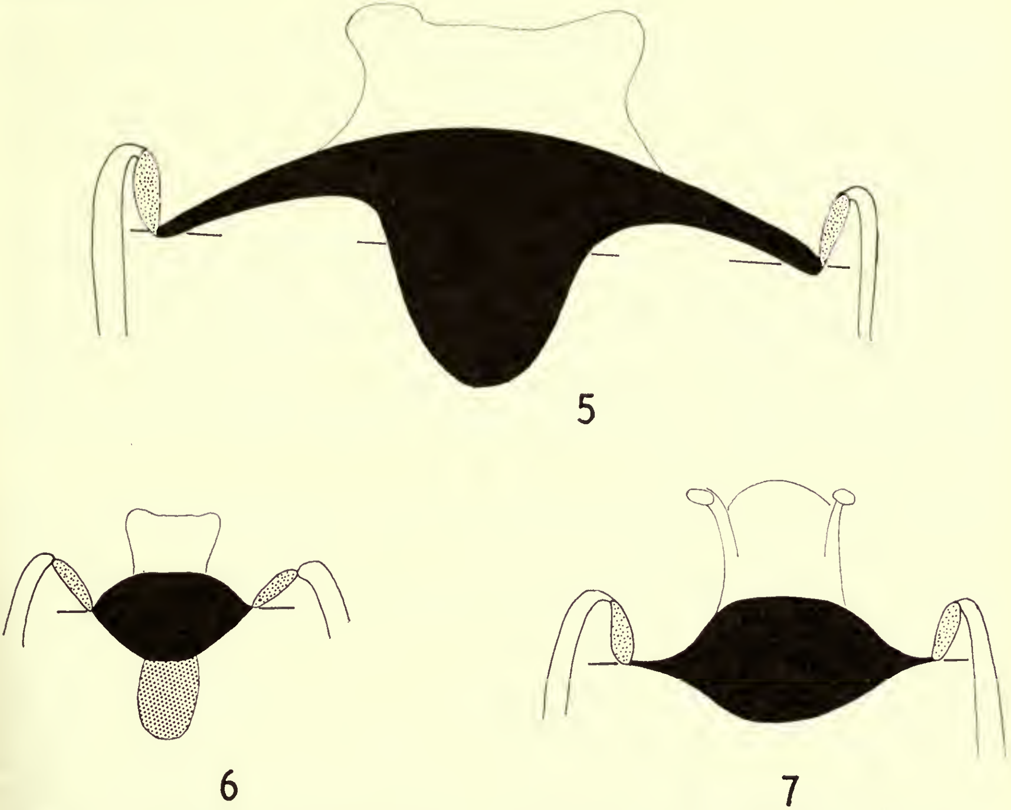


FIG. 4. The mandibular : onchial complex of one lip of a generalized Enoplidae head with complete musculature. The numbers refer to the musculature as numbered in the text on page 283.

processes. The onchial plate, therefore, represents a specialized, thickened zone of cuticle, which is slung from the radial masses (Text-figs. 5, 6, 7 and 29). The mandibular ring and the associated parts of the anterior edge of the onchial plate curve posteriorly as they pass radially towards the radial masses. Thus the points at which the plates and radial masses fuse are always posterior to the level of the cephalic ring, and generally lie on a level which is just anterior to the anterior origins of the onchia (Text-figs. 5, 6 and 7). The functional significance of this is discussed below (page 285).

In *en face* view the mandibles are curved to correspond to the curvature of the buccal cavity and the nerves which supply the labial sense organs always lie in the same relationship to them. That is, the nerves run anteriorly along a line running antero-posteriorly behind the dorso- and ventro-lateral components of the cephalic sense organs. Just posterior to these setae the nerves curve towards the interlabial spaces and run to the labial sense organs along the line of, and in close association with the edges of the mandibles (see Text-figs. 30, 31, 72, 74, 79, 84, 87 and 91). This arrangement is absolutely constant no matter how the mandibles may be modified. The mandibles, themselves, appear to arise from two distinct sources, from a thickening of the wall of the buccal cavity to form a large median plate which is flanked by rods of thickened cuticle which are associated with the nerves supplying the anterior sense organs. This is most clear in *Enoplolaimus mus* (Text-figs. 60, 61, 68 and 72) and *Oxyonchus ditlevseni* (Text-figs. 55 and 59) in which the mandibles are not as fully fused to the onchial plates as they are, for example, in *Mesacanthion* (Text-figs. 79 and 84) although even in this latter genus a *mandibular rod* component can be identified. In *Enoplolaimus mus* the mandibles, when viewed from the external or internal surface of the lip, arise from the level of the mandibular ring as a thickening of the cuticle on the mid-line of the lip (Text-fig. 61). More anteriorly two flanking rods separate from the central mass, the *mandibular plate*, and these two rods curve inwards and become pointed as the claws of the mandibles (Text-figs. 61 and 72). This is even clearer in *en face* view (Text-figs. 63, 64, 65, 66 and 67) where it can be seen that the mandibular plate not only curves circumferentially, independent of the mandibular rods, but also curves inwards anteriorly so that the plate forms a cup-like recess in the inner surface of the lip. In forms such as *Mesacanthion* the rod component is not so distinctly separate and has become incorporated into the main mass of the mandible except at its anterior end (Text-figs. 79 and 84) while in *Africanthion* no trace of a rod element is present (Text-figs. 91, 95 and 98). No distinct rod element can be seen in the mandibles of *Trileptium ayum* (Text-figs. 100 and 101) nor in *Thoracostomopsis carolae* (Text-figs. 104 and 107), but in the latter genus this could be over-looked because of the very small size of the head. Finally, when the head is considered in *en face* view, the cross sectional shape of the buccal and onchial cavities varies from one level to another. In general the buccal cavity is circular in transverse section at its anterior end but extends along the lines of the radii until at the level of the mandibular ring it is roughly triangular in section. Posterior to this ring the onchial cavity is triangular in section and the oesophageal sectors, from the anterior ends of which the onchia arise, slowly extend inwards until the typical tri-radiate condition of the oesophageal lumen is wholly established. The most important result of this alteration in the shape of the combined cavities is that the onchial plates, the mandibular ring and the radial processes tend to form a straight line in transverse section.



FIGS. 5–7. Outlines of the mandibular : onchial-plate : radial mass complex in *Mesacanthion studiosa* (Fig. 5), *Enoplus harlockae* (Fig. 6) and *Enoplolaimus mus*. Note the backward sweep of the mandibular ring and radial processes and the level at which they are attached to the radial masses.

The degree of development of these various skeletal components of the head varies from genus to genus and the detailed structure in each of the genera I have studied is as follows:

Enoplolaimus: the cephalic capsule is rather short and the outer circle of cephalic setae arises from about midway between its anterior and posterior limits (Text-figs. 60 and 62). The onchia are small and lie mainly posterior to the mandibular ring. The onchial plates are poorly developed and the radial pieces are small. The onchial cavity is deep and narrow and gives the appearance (Text-fig. 60) referred to by Wieser (1953) and Mawson (1958), in some species of the genus *Mesacanthion*, as pocketed. Whether this is a constant character or is a functional distortion I do not know but all the specimens of *E. mus* have this appearance. It should be noted that this " pocketing " is due to the radii of the onchial cavity seen in optical section and reflects the fact that the sectors of the oesophagus are narrow at this level. The cephalic ring is well developed and the head anterior to it is short and stout (Text-figs. 60 and 62). The mandibles are not wholly fused so that all the component parts—the mandibular rods and mandibular plate—can be seen. There are two large, squarish cuticular thickenings developed in the cuticle covering the *outer* surface of the head which appear to function as supports for the rather massive labial setae (Text-figs. 62, 67 and 72). The inner surfaces of the lips carry semi-lunar striations (Text-figs. 61 and 72).

Africanthion: the mandibles are lightly built with no indication of mandibular rods (Text-figs. 91, 95 and 98). The onchia lie wholly posterior to the mandibular ring and the lips are high and narrow. The dorsal onchium is slightly smaller than the two equal ventro-lateral and the cephalic capsule is short with the outer cephalic setae arising from its mid-level (Text-figs. 91 and 98). In optical section the edges of the mandibles appear as thin, light rods (Text-figs. 91, 95 and 98). The inner surface of the lips carries semi-lunar striations and the cephalic slit is small. The radial pieces are well developed.

Mesacanthion: the cephalic capsule is prominent with distinct granulations, forming a kind of cervical capsule, in the cuticle posterior to it (Text-figs. 74, 80 and 86). The outer cephalic setae arise from near the cephalic ring (Text-figs. 74, 76, 80, 84, 86 and 87). The mandibles are short, broad and massive, almost completely fused. The mandibular rods appear to be represented by two small cuticular lobes on the outer edges of the mandibles (Text-figs. 79, 80 and 84). The onchia are small and equal and lie wholly posterior to the cephalic ring. The onchial plates are very closely integrated with the mandibles so that there appears to be only one massive cuticular structure present with very distinct radial processes (Text-figs. 74, 84 and 89). The radial pieces are well developed. The mandibular/onchial plate complex is pierced by holes of undifferentiated cuticle so that they have a rough, unfinished appearance (Text-figs. 74 and 84).

Trileptium : the cephalic capsule is lightly built and the outer cephalic setae arise from its posterior edge (Text-fig. 101). The onchial cavity is large and the equal onchia extend anteriorly almost to the anterior limits of the mandibles within which they largely lie. The mandibles are small and compact, showing no indication of any component parts. They appear to act as an enclosing frame for the onchia (Text-fig. 101) which they enfold very closely when the head is viewed from the outer surface. The lips bear semi-lunar striations on the inner surface. The lumen of the mandibular cavity is tri-radiate in transverse section (Text-fig. 99) and not large and triangular as in most of the other head forms.

Oxyonchus : the cephalic capsule is fairly short and the cephalic setae arise from near the cephalic ring (Text-fig. 55). The ventro-lateral onchia are large and extend anteriorly beyond the cephalic ring while the dorsal onchium is short and does not extend so far anteriorly (Text-figs. 55, 57 and 59). The mandibular rods are very distinct and the long, transversely narrow mandibular plate bears a series of small denticles arranged in two to three rows. Any definite description of these structures as being in two or three rows is not possible as their arrangement is not regular. The cephalic slits are represented by cirri (Text-figs. 57 and 59). The inner surface of the buccal cavity is marked by semi-lunar striations and large square thickenings of the outer cuticle of head are associated with the labial setae, as in *Enoplolaimus* (Text-fig. 59).

Thoracostomopsis : the structure of the head in this genus has been misinterpreted in the past. Ditlevsen (1919) and Filipjev (1927) both refer to the difficulty they had in analyzing the structure of the head and this I can well understand since it is very easy to make the error of describing a spear—as both these authors do—in the buccal cavity when studying the specimens from the side. However, when an *en face* preparation is studied the presence of three long structures in the mouth cavity is quite clear. In view of the other great similarities between the specimens I have studied and the descriptions given by both Ditlevsen and Filipjev I have no doubt that the conditions I found are also present in the species described by these authors. The cephalic capsule and ring are very distinct and the capsule is very strongly divided on its posterior edge to form six rounded lobes (Text-figs. 103 and 109) of which the dorsal and ventral are larger than the paired laterals. Filipjev (1927) describes three " . . . plaques indépendantes, correspondantes aux trois secteurs oesophagiens." in *T. galeata* Filipjev, 1927 ; describes the capsule in *T. ditlevseni* Filipjev, 1927 as poorly developed and reports his inability to make out the details of the structure of the capsule in *T. longissima* Filipjev, 1927. Ditlevsen (1919), however, shows a capsule which is almost identical with that figured here. Filipjev (1934), in spite of his own and Ditleven's descriptions, describes the capsule in this genus as four-lobed, this is clearly an error. The head, anterior to the cephalic ring, is long and narrow and, as a concomitant, the cephalic ventricles are also long and narrow. The mandibles are also long and narrow with no apparent trace of their component parts. This is difficult to establish definitely because of the small size of the anterior part of the body. The cephalic setae arise about half way up the cephalic capsule (Text-figs. 103, 104 and 109). The onchia are very long, thin and sheet-like. The anterior part of the oesophagus is modified as a distinctly swollen region (Text-figs. 103 and 104) from which the modified onchia arise. The onchia extend anteriorly to about the anterior ends of the mandibles and, although they merge slowly into the oesophagus over the entire length of the anterior modification, their anterior line of origin is clear (Text-fig. 104). In *en face* view the onchia are seen to fold round each other to form a tube (Text-figs. 105 and 106). In the specimen studied *en face* the arrangement is as shown in Text-fig. 106 with the dorsal onchium enfolding the two ventro-lateral which in their turn overlap so that a distinct tube is formed. The head in this genus is, therefore, made up of the same components as all the other, more typical, members of the Enoplidae.

Enoploides : I have been able to study only one larval specimen of this genus and it shows the following combination of structures. The cephalic capsule is lightly built and all the sense organs are setose. The lips are large with terminal lobes and are marked internally by fine semi-lunar striations. These striations, as is usual, stop along a curved line originating at the slightly protruding tips of the mandibles (Text-fig. 30) and the outer edges of the lips beyond this line, are further marked by striations which are much further apart than the semi-lunars. The mandibles are narrow and solid looking. The onchia are small and arise from a somewhat thickened onchial plate. The division between the onchial and mandibular components of the mouth armature is clear (Text-fig. 30). The radial pieces are well developed (Text-fig. 29) and the cephalic ventricle is somewhat reduced. There is a supporting piece developed in the outer cuticular covering of the head which is associated with the mandibles (Text-figs. 29 and 30). There is no obvious cephalic ring.

Rhabdodemania : this genus is considered here for convenience (see discussion later, page 322). As Wieser (1959) suggests, the " cuticular projections " and the " three pairs of longer onchia " usually described for this genus may be interpreted as homologous with the onchia and mandibles, respectively, found in more typical Enoplidae. An *en face* preparation established this beyond doubt (Text-fig. 116). In the species I describe later (*R. nancyae*, page 322) the mouth opening appears to be large and circular but it is difficult to be sure as the specimens are in a somewhat poor condition, but the lining of the mouth opening is striated. Wieser (1959) refers to " . . . strongly developed, cushion-like lips " but he is clearly referring to the stout, projecting anterior end of the body (Text-fig. 117). A very poorly developed cephalic capsule may be present but once again I cannot be sure. Nevertheless the cuticle at the anterior end of the body is very thick and the oesophagus is fused to it for some distance back from the anterior end (Text-figs. 117 and 121). I would interpret the outer striated part of the mouth cavity as being homologous with the buccal cavity of more typical forms. The next part, that is the thick cuticle lying anterior to the end of the oesophageal musculature and posterior to the striated capsule, I interpret as the highly modified mandibles while the cavity posterior to this (in which in my species there is a large dorsal and two very small ventro-lateral onchia) as the onchial cavity. The labial sense organs are papillae and the cephalic are setae in one circle.

Enoplus : the cephalic capsule is short and without incisions or fenestrae. The cephalic setae are short and stout in one circle and the labial sense organs are papillate. The cephalic ventricle is almost completely reduced in association with the loss of onchia and the onchial cavity and the general shortening of the mandibles and lips. The cephalic ring is very prominent. The mandibles are narrow and, in association with the onchial plate, appear to form one massive, dense median structure at the anterior end of each sector of the oesophagus (Text-fig. 110). The entire inner surface of the buccal cavity appears to be striated as in *Enoploides* and the oesophagus is fused to the cephalic capsule along three zones which correspond to the three sectors of the oesophagus over most of the length of the capsule (see Inglis, 1962). The lumen of the buccal cavity is tri-radiate. The whole head, in fact, represents a condensation of the components present in the other members of the family with a great reduction of all the cavities and structures. It should be noted that the onchial plate can still be distinguished from the mandibles (Text-fig. 31).

MUSCULAR COMPONENT OF THE ENOPLIDAE HEAD

The anterior end of the oesophagus is modified into a number of distinct muscles which are attached mainly to the onchial plates. All the muscles are the result of specialization of that part of the oesophagus which corresponds to the cephalic capsule and are arranged in two transverse rings within the anterior part of the oesophagus. They are arranged in the same way in all the three sectors of the oesophagus so that the description of the set corresponding to one sector of the oesophagus applies to all three. All the muscles are inserted on the onchial area, none are inserted on the mandibles, no muscles originate from outside the oesophagus and all the muscles have their origins on the outer surface of the oesophagus. The arrangement of these muscles is very constant throughout the various species I have studied. I have been unable to find any previous record of the form and distribution of these muscular specializations so that I can only discuss the range of modification in the species I have seen. The arrangement of the muscles is most easily understood from text-figs. 3 and 4. In each sector of the oesophagus there are three muscles in the anterior ring and four muscles in the more posterior. The origins of the more anterior muscles extend posteriorly to pass between the origins of the components of the more posterior ring (Text-figs. 4, 13, 20, 23, 28 and 33). These muscles will be discussed under numbers, thus : MUSCLE-1 is the median, unpaired muscle of the anterior ring, MUSCLE-2 occurs as a pair of muscles of the anterior ring, one on each side of Muscle-1. MUSCLE-3 occurs as a median pair in the more posterior ring and they are separated from each other by the tail of the origin of Muscle-1. Flanking Muscles-3 is a further pair, MUSCLE-4, which are sometimes very difficult to locate in dorsal or ventro-lateral view and are sometimes partly separated from Muscles-3 by the tails of the insertions of Muscles-2. (Text-figs. 13 and 20). The muscles of the anterior ring, Muscles-1 and -2, run anteriorly and inwards to insert on the onchial plate just posterior to the mandibular ring. They are thin posteriorly and become increasingly stouter and broader anteriorly. Muscles-2 are always smaller and shorter than Muscles-1. Muscles-3 insert on the posterior part of the onchial plate and are the most massive component of the musculature (Text-figs. 13, 20, 23 and 28). They are, in longitudinal section, somewhat fan-shaped running inwards to insert over a rather small posterior area of the onchial plate (Text-figs. 14, 17, 19, 25, 27 and 32). Muscles-4 insert on the thinner cuticle which flanks the onchial plate and lines the more radial parts of the onchial cavity (Text-figs. 4, 10, 12, 14, 15, 19, 25, 27 and 32). Posterior to these specialized muscles the oesophageal musculature runs wholly radially but is divided into two blocks in each sector by the lumen of the duct of the oesophageal gland (Text-figs. 9 and 35). Muscles-3 and -4 first appear at about the level at which the gland ducts narrow to form the relatively fine terminal portion. The lumen of the oesophagus expands very quickly at the same level, to form the onchial cavity, by the disappearance of the axial parts of each of the oesophageal sectors (Text-figs. 9 and 27). Thus, in longitudinal section the onchial cavity appears as a step in the outline of each oesophageal sector. The transition from the wholly radial arrangement of the muscles to the two rings of specialized muscles is fairly abrupt with no obvious zone of transition. As the oesophageal duct narrows the sheets of muscle flanking it extend slightly and then the specialized musculature begins. In transverse section the foramina through which pass the nerves to the cephalic sense organs always lie between Muscles-3 and -4 (Text-figs. 12 and 25). The general arrangement of the muscles, with their directions of action is shown in Text-figs. 3 and 4. This arrangement is present in all the species I have studied although there is some variation co-related with the degree of fusion or development of the various skeletal components of the head. Thus, in *Mesacanthion* (Text-figs. 9–17) all the muscles are very prominent with a slight suggestion that Muscles-4 are divided into two parts. This appears to be due to the foramina through which pass the nerves supplying the labial sense organs (Text-fig. 11). In *Enoplolaimus* the Muscles-1 and -2 appear to be much more closely packed together anteriorly, associated with the much narrower anterior edge to the onchial plate ; this is, in its turn, associated with the narrow mandibles (Text-fig. 20). Also in transverse sections, Muscles-3 and -4 are rather slim and lie far apart (Text-fig. 19). In *Africanthion*, although all the muscles are clearly present, because of the poor condition of the specimens I have been unable to establish the exact arrangements of Muscles-2 so that the conditions shown in Text-fig. 23 are only approximate. However, as is clear from Text-figs. 24 and 25, as far as it is possible to establish, the musculature is the same in principle as that previously described. The radial masses are very well developed (Text-fig. 25) and Muscles-4 are relatively massive in comparison to Muscles-3 while the musculature of the oesophagus surrounding the anterior part of the gland duct is very lightly developed (Text-fig. 25). In *Trileptium* the same arrangement of muscles occurs with the major difference that Muscles-4 stop relatively far posteriorly, probably in association with the great development of the radial masses. In this form the oesophagus is attached to the cephalic capsule along three zones for a large part of the cephalic region. In *Enoploides* Muscles-1 and -2 appear to fuse anteriorly to form one sheet and Muscles-3 are separated by the tails of all the muscles of the anterior ring (Text-fig. 28). That is, the posterior parts of the origins of Muscles-2 lie between the origins of Muscles-1 and -3 instead of between Muscles-3 and -4 as in, for example, *Mesacanthion*. Finally in *Enoplus* Muscles-1 and -2 are completely fused, except for a possible slight indication of a division near the anterior edge in some specimens (Text-fig. 33), to form one muscle mass which is flanked by long, narrow Muscles-3 which in their turn are flanked by Muscles-4. The general arrangement of the muscles, is however, the same as in all the other groups. That is, the large anterior muscle, Muscle-1/2 sheet, is inserted on the onchial plate just posterior to the mandibular ring while Muscles-3 are inserted at the posterior edge of the onchial plate and Muscles-4 are inserted on the lining of the oesophagus bordering the onchial plate.

FUNCTIONAL ANALYSIS OF THE ENOPLIDAE HEAD

The complex structures found in the head in the family Enoplidae are all functionally interrelated. The most obvious morphological feature of the head is the massive mandible : onchium system which must function as a unit although the component parts are derived from different sources. All the muscles are attached to this complex posterior to the mandibular ring which represents the posterior limit of the mandibular component of the complex. Thus the Muscles-1 and Muscles-2 will act so as to pull the mandibles outwards and backwards while causing the onchia and onchial plates to move inwards and forwards. Muscles-3 will act in apposition to these and on contraction reverse the movement, pulling the onchia and onchial plates posteriorly and outwards while causing the mandibles to move inwards and posteriorly (Text-fig. 8). The role of Muscles-4 in this is not clear. They do not appear to be essential, in view of their great reduction in *Trileptium*, but might act simply to re-inforce Muscles-3. It appears more probably, however, that Muscles-4 simply act to dilate the lumen of the oesophagus near its anterior end and so may be considered to correspond in action to the unspecialized oesophageal musculature found more posteriorly. The onchial plate is the development of the inner cuticle at the anterior end of the oesophagus on which the specialized muscles, 1, 2 and 3, have their insertions while the cephalic capsule corresponds to the part of the oesophagus from which they have their origin. The most immediate question is, round what point do the complexes rotate ? At first it is difficult to see how such a system can rotate under the action of the muscles. However, when the form of the onchial plate is studied, most easily in specimens under pressure, it is not a symmetrical structure but is curved posteriorly along its anterior edge. Thus the radial processes are directed slightly posteriorly (Text-figs. 5, 6, 7 and 30) and the entire complex is slung from the radial masses at two points which lie mid-way between the two rings of muscles so that they can act in apposition (Text-figs. 5, 6 and 7). This can also be seen when the radial masses are studied from the outer surface of the head. Although the lips fuse externally relatively far anteriorly there is no fusion of the internal structures for some considerable distance posterior to this point. That is not until the level, roughly, of the radial processes. This arrangement is present in all the species studied and is also well shown in Ditlevsen's (1919) figure of *Enoplolaimus latignathus* (Ditlevsen's Plate XIII, Fig. 1). Thus the mandibular : onchial complex is slung from the radial masses so that the rotation line passes between the insertions of Muscles-1 and -2 and those of Muscles-3. The mandibles, therefore, are rotated under the action of muscles on the onchial plate and do not themselves have any muscle supply. The arrangement of the muscles of the anterior ring, Muscles-1 and Muscles-2, may indicate that they have arisen in response to the presence of three components in the mandibular complex but it is not possible to establish, or refute, this possibility until a more divided complex has been studied. I suspect, rather, that the arrangement of the muscles is determined first by the presence of the duct of the oesophageal gland which divides the oesophageal musculature into two blocks and more anteriorly the presence of the onchia causes a division into four—Muscles-3 (two) and Muscles-4 (two)—and finally the most anterior muscles, Muscles-1 and Muscles-2, are arranged so as to fit into the more posterior muscles so that the available space is fully utilized.

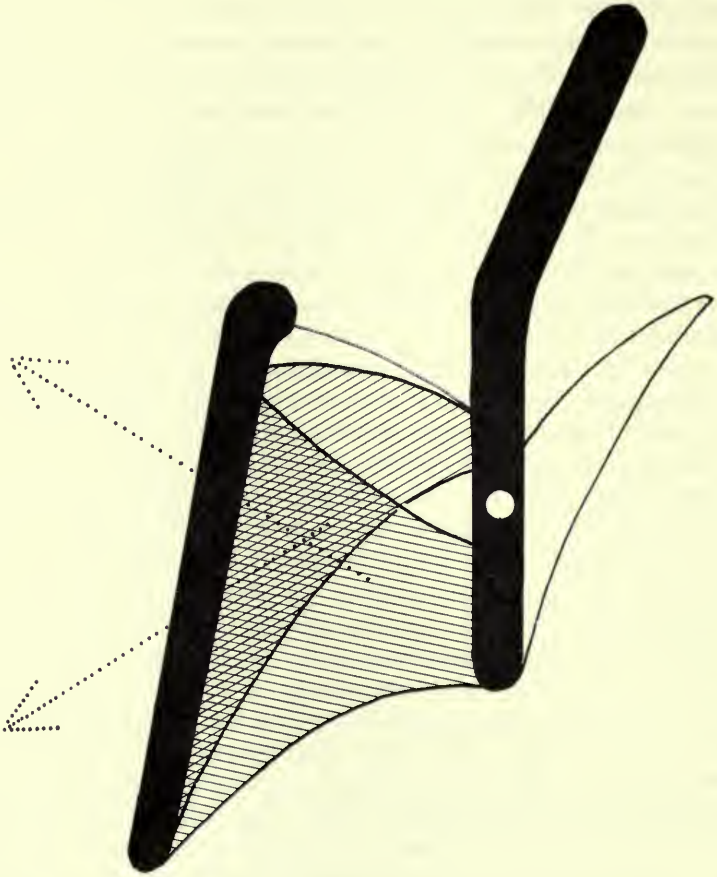


FIG. 8. Diagrammatic arrangement of the musculature of the mandibular : onchial-plate complex in the Enoplidae. The complex is to the right of the figure, the white dot represents the point of rotation of the complex and the arrows represent the approximate lines of action of the muscles.

THE STRUCTURE OF THE HEAD IN THE LEPTOSOMATIDAE

The structure of the head in this family has been considered by Wieser (1954) but, as pointed out above, he has over-looked some structural detail, particularly the presence of the cephalic ventricle, and I cannot accept his terminology and treatment of the so-called stomadaeal capsule. In general the head in this family is similar to those described in the other two families with a cephalic capsule and, in some cases, particularly *Thoracostoma*, there is a prominent cephalic ventricle.

The cephalic capsule in some genera is very strongly developed and a very distinct oesophageal capsule can also be present, for example in *Thoracostoma, Cylicolaimus, Macronchus*. In some cases a granular cervical capsule is also present. The elaborate arrangement of mandibles and onchia characteristic of the Enoplidae is never present. The most marked difference between this family and the others is in the way the musculature which supplies the various elaborations of the short buccal cavity extends anteriorly through the cephalic ventricle beyond the oesophageal capsule. To consider the structure of the head in the various species I have studied, in *Anticoma chitwoodi* there is a distinct cephalic capsule which, in one specimen, is pierced by several *lacunae* (Text-figs. 125–131). There is no cephalic ventricle and there is a single small onchium on each sector of the oesophagus (Text-figs. 122 and 125). There are no marked incisions in the cephalic capsule although in some cases the narrow fenestrae through which the nerves supplying the labial sense organs pass can be seen below the capsule. In *Parabarbonema* the cephalic capsule is well developed, without incisions. The amphidial openings lie on the posterior edge of the capsule, as in *Anticoma*, there is a slight cephalic ventricle, the mouth opening is tri-radiate and bounded by slight lip-lobes, the anterior end of each sector of the oesophagus is modified as a slight onchium which takes the form of a ridge of cuticle extending round most of each sector and the buccal cavity is very short (Text-figs. 132 and 133). The musculature which supplies the onchia can be seen arising within the anterior end of the oesophagus (Text-fig. 133) but due to the small size and poor condition of the specimens I have been unable to study its distribution in detail. It does, however, appear to represent a simple modification of the middle region of the musculature at the anterior end of each sector of the oesophagus. There are no incisions but six thin channels can be seen under the thickened cuticle of the cephalic capsule. There are six small lobes on the anterior edge of the cephalic capsule which lie in line with these fenestral channels (Text-figs. 132 and 133). The labial sense organs are papillate while the cephalic are setose (Text-fig. 137).

In *Macronchus* the cephalic capsule is very prominent but relatively narrow (Text-figs. 138, 139 and 141), there is a well developed oesophageal capsule and cephalic ventricle, the mouth opening is bounded by three lip-lobes (Text-fig. 143) and there is a large onchium developed from the middle of each oesophageal sector (Text-figs. 138 and 143). The muscles which supply the onchia form one mass, arising from the middle of each sector of the oesophagus at its anterior end, which passes anteriorly through the cephalic ventricle, as in *Parabarbonema*. The lining of the oesophageal lumen is strongly thickened at its anterior end (Text-fig. 141). The cephalic capsule has very slight incisions on its posterior edge and six fenestral channels can be seen beneath it. The onchia are flanked by a series of prominent wholly cuticular denticles which arise from a continuous basal sheet of cuticle which lines the shallow buccal cavity and is independent of the onchia and the oesophagus (Text-figs. 138, 139 and 141). In *en face* view, in deep focus, the distribution of the musculature which supplies the onchia can be seen rising as a mass from the middle of each sector of the oesophagus which is flanked by the spaces of the cephalic ventricle (Text-fig. 140). In addition there is a narrow dense strip of cuticular material running from the outer end of each radius of the oesophagus to the periphery of the oesophagus. This structure is probably homologous with the radial mass in the Enoplidae. The result of the combination of these six structures, three muscle masses—which it should be noted are lying wholly within the head and do not project into the buccal cavity—and three radial strips, is that each nerve passing anteriorly comes to lie in a triangular space of the cephalic ventricle.

In *Thoracostoma* the cephalic capsule is very strongly developed with a prominent system of incisions, fenestrae and, in most cases, lacunae. The cephalic ventricle is very well developed and there appears to be a well developed oesophageal capsule in many cases. The oesophageal capsule and cephalic capsule are fused completely round their circumferences only at the anterior end and are attached to each other along three zones, which correspond to the three sectors of the oesophagus, posteriorly. Narrow strips of dense material run from the ends of the radii of the oesophageal lumen to the periphery of the oesophagus as in *Parabarbonema*. The anterior end of the oesophagus and the lining of the shallow buccal cavity are modified to form a variety of structures but when any of them is supplied with musculature this always arises from the anterior end of the oesophagus and passes forward as a narrow strip through the cephalic ventricle (Text-figs. 152 and 153). There are, therefore, two components in the anterior buccal armature, a true onchial one—such as the large bifurcate dorsal onchium in *T. jae* (Text-fig. 157)—and a buccal. In forms such as *T. zeae* (Text-figs. 171 and 172) the large central structure on each ventro-lateral side of the buccal cavity is an onchium while the smaller flanking structures are derived from the cuticle lining the buccal cavity. Similarly the two ventro-lateral structures in the mouth of *T. jae* are onchia. The muscle supply to the similar large onchial structure developed on the dorsal side of the oesophagus is also shown by Wieser (1956, Fig. 1, c. page 245) in *T. bruuni* Wieser, 1956. In addition, in all three species there is a second, more posterior, wholly cuticular onchium developed from the covering of the dorsal sector of the oesophagus (Text-figs. 150, 154, 167 and 173). The anterior edge of the cephalic capsule is developed into six anteriorly directed lobes which correspond to the position of the nerves supplying the labial, papillate, sense organs. Wieser (1953 and 1956) refers to various lobes developed on the anterior edge of the cephalic capsule and six such structures are present on all three species I have seen. They are in all cases slightly serrate on their anterior edges the impression being that they are thinning and disappearing rather than that this reflects any specific character in their organization. The structure of these anterior lobes is difficult to establish with certainty since there appears to be an inner lobe from the oesophageal capsule accompanying them. I have shown such a structure in the figures (Text-figs. 152, 153, 167 and 168) but cannot be certain of its independent presence since it may simply represent the edge of the cephalic capsule lobe in optical section. The structure marked " stomadaeal ring " in Wieser's 1956 figures is the anterior part of the thickening of the oesophageal capsule seen in optical section and is not a distinct ring as in, for example, *Enoplus*. The cephalic ring is, in all the specimens I have seen, a rather thin, lightly built structure (Text-figs. 150, 154, 168 and 169) which can only be seen with difficulty. The shape of the cephalic capsule and its associated incisions, fenestrae and lacunae has been used as major character in the delimitiation of the various species of *Thoracostoma* but the extreme variation in some of the characters can be seen from Text-figs. 159–166 and 176–179. The systematic value and interpretation of these characters is considered fully later (page 330).

Two points remain to be considered. Schuurmans Stekhoven and Mawson (1955) and later Mawson (1958, 1958a) describe " three anterior processes from the helmet which come into relation with the stomatal lining at the angles of the buccal cavity " (Mawson, 1958a). I have not seen any such processes but they would appear to be represented by the cuticularization which stretches from the ends of the radii to the outer surface of the oesophagus. I would, therefore, interpret them as derivations from the oesophagus comparable to the radial masses of the Enoplidae. This is, however, by no means certain but it would appear to be most improbable that they are developments of the cephalic capsule itself. One result of this modification, however, is that anterior to the cephalic ring the vesicle is divided into six parts which are separated by the radii of the oesophagus and the structures connecting them to the outer surface and by the three anteriorly directed lobes of the oesophagus which supply the onchia (Text-figs. 156 and 173). It is this combination of characters which gives rise to the second point I wish to consider. Timm (1953) describes the presence of " six pairs of fine sclerotized pieces symmetrically arranged" round an anterior " cap " of oesophageal tissue in the female of *Leptosomatum acephalatum* Chitwood, 1936 and later describes similar structures from both sexes of *L. ranjhai* Timm, 1960. De Man (1893) describes similar structures from *L. elongatum* and Mawson (1958a) describes them from what she considers to be *L. arcticum* Filipjev, 1916. However, Timm (1953) points out that " The sclerotized pieces as figured appear broader than in totomount view due to their refractiveness when traced up and down.", this being in " The second cross section at 6μ. . . ". I am quite sure that what Timm is describing here is the same system as is shown in Text-figs. 156 and 173, that is, the lining of the cephalic ventricle, one component of each pair of sclerotized pieces corresponding to the musculature supplying the onchia and the other component corresponding to the radius of the oesophagus.

GENERAL DISCUSSION OF THE STRUCTURE OF THE HEAD

The structure of the head forms considered above may be treated as falling into two major groups which correspond to the two major forms of the oesophagus. The Enoplidae and Phanodermatidae in which the oesophagus is distinctly " cellular" or (another term) " Vesiculate " posteriorly and the Leptosomatidae in which it is wholly muscular posteriorly. The cellular appearance is easily recognized and is due to the musculature being concentrated into distinct bands. In the first two families the musculature of the oesophagus never extends anterior to the anterior limit of the cephalic capsule and the onchia, if present, always appear to project into the buccal or onchial cavities free from the surrounding structures. In the

Leptosomatidae the musculature of the oesophagus extends anterior to the cephalic ring, through the cephalic ventricle, the buccal cavity is relatively reduced and the musculature inserts inside the onchia and does not simply attach to the base as in the Enoplidae/Phanodermatidae—at least in the most highly specialized forms. The easiest way to see this difference is to compare the way in which the musculature is cut off sharply at the anterior end of the oesophagus in *Mesacanthion* (Text-figs. 16 and 17), for example, and how it extends anteriorly in, for example, *Thoracostoma jae* (Text-figs. 152 and 153). As a result the onchia in the Leptosomatidae tend to be carried much more anteriorly, relative to the mouth opening, than they are in the Enoplidae and Phanodermatidae so that the buccal cavity in the first family is shallow, but is deep in the other two families.

The primitive head form can be considered to be represented by the simple attachment of a form such as *Anticoma* with a cephalic capsule but no cephalic ventricle or any of the systems of rods or other elaborations. Such a head would probably have, or is best considered as having, a tri-radiate mouth opening without lips. Under such conditions the extent to which the mouth could open would depend on the opening of the lumen of the oesophagus, as is certainly true in, for example, some members of the Oxystomidae. As I have argued in considering the Subuluridae (Inglis, 1960), since the oesophagus acts as a pump and is a relatively dense organ, first the size of the particles which can pass down the lumen must be limited to the size of the open lumen and second the size of the mouth opening and the cross-sectional area of the buccal cavity must control the size of particle which can pass inwards to the oesophagus. Doncaster (1963) makes the same point about *Rhabditis oxycerca* and *Pelodera lambdiensis*, " The size of those (microbes) injested is limited by the diameter of the stoma". Now in the simple head of the *Anticoma* or *Crenopharynx*-type there is no such method of selection available and it appears certain that there is an evolutionary advantage in the appearance of such a preliminary sampling zone. In addition the simple mouth opening must have little flexibility. This would also be improved by separating the mouth opening and the oesophagus. The separation of the mouth opening from the oesophagus is very common throughout the Nematoda but only in the Enoplida has a large cephalic vesicle appeared (although a similar modification appears to be present in many Tylenchida) and its appearance is probably casually related to the fusion of the oesophagus to the body wall (a similar modification appears to be present in the Tylenchida also). If an evolutionary trend from forms without to forms with a buccal cavity be accepted, as appears to be incontrovertible, whether on the line of the Phanodermatidae/Enoplidae or the Leptosomatidae, I would argue that the buccal cavity appeared by a migration outwards of the tissue lining the inner surface of the buccal cavity. Because of the presence of the fusion of the oesophagus and body wall this tissue would have been unable to extend its movement beyond the line of attachment so that it built up at the anterior end of the body to form the cephalic ventricle. The development of such a vesicle necessitates the development of some kind of supporting structure, particularly for the inner circle of sense organs, and this is represented by the buccal rods of *Dayellus* and *Phanoderma*. The origin of such rods is probably indicated by the conditions in the head of *Crenopharynx* in which precursors of rods appear to be represented by the cuticular V-shaped structures flanking the oesophageal radii at its anterior end. Further increase in the depth of the buccal cavity with an increase in the density of its lining would produce a mandibular plate, the independence of the buccal rods (mandibular rods) is reduced, the mandibular component becomes functionally the dominant part of the system, the onchia are reduced and finally disappear with a concomitant reduction in the depth of the buccal cavity and the size of the cephalic ventricle. An originally supporting system becomes the major triturating system to the exclusion of the original system which is now reduced to acting as the area of insertion for the muscles which operate the mandibles.

To elaborate, I interpret the six-lobed mouth opening of *Phanoderma* as derivable from a three lobed system similar to that of *Crenopharynx*. Thus the pre-cursors of the buccal rods would be localized by the coalition of the ends of the radii of the oesophagus and the associated part of the buccal cavity. In *Dayellus* the presence of prominent buccal rods in association with a large cephalic ventricle is clearly seen while in *Phanoderma* the rods are still present although the ventricle is somewhat reduced. It is clear that these three head forms cannot be considered to represent any kind of series since, although *Phanoderma* could be derived from *Crenopharynx* by an increased cuticularization of the anterior end of the oesophagus, *Dayellus* appears to represent a specialized form in which the onchial component of the oesophagus is greatly reduced. It is difficult to draw any general conclusions about this family in view of the very small number of forms referred to it and the insufficiency of most of the descriptions of the head. Some minor observations on the relationships within it will be found in the systematic section of this paper (page 305).

The structure of the Enoplidae head, although it forms a remarkably uniform group, can be considered as an elaboration of the type found in the Phanodermatidae. Thus, if the sheet of cuticle lying between the buccal rods of the Phanodermatidae should become thicker and denser an Enoplidae head would, in broad outline, result. This I think is what has happened. With an increase in the size of the head the mechanical requirements of supporting the cuticle surrounding the buccal cavity would necessitate the development of an increase in the skeletal component and this is what the mandibular complex clearly does. That it also acts, in most cases, as a system of gripping organs or jaws cannot be doubted but its arrangement within the lips and its fixed relationship to the nerves and labial sense organs can best be interpreted as those of a skeletal system. With the development of such a skeletal system the appearance of massive buccal and onchial cavities is rendered possible with the associated complex of onchial plates, radial processes, radial masses and specialized musculature. With an increase in the thickness of the specialization of the wall of the buccal cavity the importance of the buccal/mandibular rods must be reduced as their functions are progressively taken over by the mandibular plate until they become fused with it, as in *Enoplolaimus*, and finally absorbed into it, as in *Mesacanthion* and *Africanthion*.

With the development of the mandibular : onchial complex a new level of organization has been reached which has enabled a massive radiation to occur resulting in heads without onchia or onchial cavities and reduced buccal cavities as in *Enoplus*, heads in which the onchial cavity has become dominant with a reduction of the onchia, mandibles and buccal cavity, as in some *Trileptium*, heads in which the mandibular cavity has become dominant with a reduction in the size of the onchial cavity and the onchia, as in *Rhabdodemania*, heads in which the onchial component dominates with a great reduction or even complete loss of the mandibular component, as in *Oxyonchus* and heads in which the onchial component has dominated with reduction of the other components to minor supporting roles, as in *Thoracostomopsis*. It is clear from what I have just said that I am considering a head form such as that in *Enoplolaimus* as a morphotype or at least in some way median for the Enoplidae. This is simply for convenience since it supplies a good generalized head form which shows all the morphological features of the Enoplidae head in a reasonably well developed form. But to treat this as a primitive head type would be a mistake, it is only a generalized type. Wieser (1953) illustrates what he calls " . . . some interesting trends of progressive or regressive development with regard to the structure of the buccal cavity . . . " and derives all the head forms from *Enoplolaimus*. This is not necessarily correct. It is noticeable that in the family the onchia can occur in two major ways, either they are all equal or the dorsal is smaller than the two, equal, ventro-lateral onchia. In the group with unequal onchia there are four obvious genera, *Savaljevia* Filipjev, 1927—with very poorly developed or no mandibular component and very long onchia ; *Parasavaljevia* Wieser, 1953—with a well developed mandibular component with distinct mandibular rods and very long onchia ; *Oxyonchus* Filipjev, 1927, with a well developed mandibular complex with distinct mandibular rods and shorter onchia which do not extend beyond the anterior end of the mandibular complex and *Enoplonema* Kreis, 1934, with mandibles which are well developed anteriorly and in which the onchia are short. Wieser (1953) treats this series as running *Oxyonchus* (with *Enoplonema* and *Parenoplus* as side branches)–*Parasavaljevia–Savaljevia* but there is more evidence to support the reverse interpretation, *Savaljevia-Parasavaljevia-Oxyonchus* since such a line could have originated with a Phanoderma-like form with unequal onchia and no mandibles and be thought of as a line along which the onchia have become reduced in size as the mandibular complex increased in importance. The relationship of *Parenoplus* Filipjev, 1927 to this group must, on the basis of what little evidence there is, be considered very doubtful while the status and relationships of *Enoplonema*, which is only known from Kreis's (1928) description of *Enoplonema* [=*Filipjevia*] *macrolabiatus*, must remain uncertain until a fuller and more detailed description is available. The other relationships Wieser suggests appear to be as well founded as is possible. That is, *Mesacanthoides*, Filipjev, 1927, *Enoploides* Savaljev, 1912, *Metenoploides* Wieser, 1953, and *Enoplus* Dujardin, 1845 represent a related group of genera. But I cannot understand the supposed differences between *Epacanthion* Wieser, 1953 and *Mesacanthion* Filipjev, 1927. Wieser says (on page 79) of *Epacanthion*, " The mandibles form an intermediate stage between *Enoploides* and *Mesacanthion*." but on page 58 he shows *Mesacanthion* linking *Enoplolaimus* and *Oxyonchus*. So far as I can make out the mandibles in *Mesacanthion* sensu Wieser, 1953 are similar to those I have found in *Africanthion* while those of *Epacanthion* are similar to those I have found in the three species I refer to *Mesacanthion*, but see page 310. The apparently simple arrangement of genera set out by Wieser is further complicated by the occurrence of genera such as *Trileptium* Cobb, 1933, *Hyalacanthion* Wieser, 1959 in which the middle part of the mandibles is a thin sheet of cuticle, *Rhabdodemania* Baylis and Daubney, 1926, and *Trichenoplus* Mawson, 1956 (of which *Lyranema* Timm, 1961 is clearly a synonym).

Because of this elaboration and variation in the degree of development of the various components of the head it is not possible to arrange them in any significant sub-groups or even to suggest any lines of modification which have any objective significance. Every combination of characters appears to have been developed and much more information is required before anything approaching a reasonable grouping of the forms can be attempted. It does appear possible that the head structures have arisen from more than one source. That is, that the family Enoplidae as at present constituted is artificial and includes two, or even more, convergent groups. Nevertheless, it is clear that the genera *Enoplus* and *Enoploides* represent related groups which have been derived from groups with much more prominent onchia. We have here the derivation of a group with reduced buccal and onchial cavities from forms in which these cavities and their associated onchia were well developed so that *Enoplus*, for example, represents an extreme of modification and efficiency with a most economic use of the minimum amount of material. But, since I interpret the origins of such onchiate groups with large cavities to be from forms in which such elaborations were not present, along at least one line of evolution there has been first an elaboration of the buccal and onchial cavities and a later reduction. This regression of an earlier elaboration appears to have been the result of the reversal of the direction of tissue migration. This I have argued was probably from the interior of the buccal cavity outwards in the first stage of elaboration but has probably been by an inwards movement and condensation in the second stage, leading to the loss of the onchia and the condensation of the mandibles. This inward migration of tissue reduces the size of the buccal cavity and the cephalic vesicle and leads to an associated reduction and final suppression of the onchia. It also appears to have affected the distribution of the cephalic sense organs in that there is a definite tendency for a reduced onchial: mandibular complex to be associated with anteriorly situated cephalic setae, as in *Enoplus* and *Enoploides*.

If my interpretation of the origins of the head in the Enoplidae with its later condensation in at least one line be correct it shows an interesting parallel with the conditions occurring in some parasitic forms, *Porrocaecum ensicaudatum* (Zeder, 1800), for example, in which there is the appearance of an elaborate lip-pulp in the larvae and a subsequent simplification in the adult (Osche, 1958) while Chabaud (1959) argues a similar regression to explain the structure of the head in *Tetrameres americana* Cram, 1927, and in the genus *Cyrnea*. Chabaud has, however, extended the concept to cover in the first case the structure of the head in the larvae, the male and the female and in the second the argument is applied to a sequence of species within a genus. I am extending the demonstration of this not unexpected phenomenon to apply to a series of genera.

In the Leptosomatidae the elaborate arrangement of mandibles and onchia characteristic of the previous family is never developed. This would appear to be associated with the way in which the onchia are developed from the oesophagus with musculature running anteriorly through the cephalic vesicle anterior to the cephalic ring. As a result no supporting structures have appeared in the buccal cavity, which is always small, in association with the nerves to the labial sense organs. Instead a comparable set of structures has been developed on the anterior edge of the cephalic capsule in, at least, *Thoracostoma* and *Parabarbonema.* Wieser (1954) employs the term " mandibles " in referring to the genera *Triodontolaimus*, and *Jagerskioldia* but the structures to which he refers are onchia. The further elaboration which flanks the onchia in genera such as these and *Thoracostoma* is always an elaboration of the wall of the buccal cavity and this cavity never attains the importance or size it reaches in the Enoplidae. Thus I interpret the Leptosomatidae as probably a group with little opportunity for further advance, other than minor specialization, because of the way in which the musculature of the onchia has developed. It is clear that the origins and importance of the Enoplidae, on the other hand, are dependent on the restriction of the musculature of the oesophagus to the posterior part of the head and it can—and will now—be argued that it is from this line that many of the other major groups of the Order have arisen.

Filipjev (1927) refers to the presence of pockets in the head of members of the Oncholaimidae but I have been unable to find any such structures in any of the genera of this family I have studied: *Oncholaimus*, *Prooncholaimus* (Inglis, 1962), and *Pontonema* (in this report). In all cases the musculature at the anterior end of the oesophagus is greatly reduced, in association with the development of a very large cavity, and is restricted to small strips running to the onchia (Text-figs. 184 and 185) and the inner layer of the cuticle at the anterior end of the body becomes markedly thicker from about the level of the amphidial opening anteriorly. This thickening is quite easily seen in uncleared specimens and frequently its posterior limit can be seen as a faint line running transversely round the body. Anteriorly, in *Pontonema*, the mouth capsule is fused to the outer cuticle of the body just anterior to the cephalic setae, once again showing as a faint line. This fusion does not originate along a simple transverse line but as six zones of fusion lying between the sense organs and the fusion is only complete round the head anterior to the labial sense organs. There are in effect six very wide foramina and when this region is studied the pocketed appearance described—and illustrated—by Filipjev results due to studying two zones of the head in optical section. The cephalic capsule is, therefore, still represented in this family by a thickening of the inner cuticle although the zone of attachment of the oesophagus and body wall has been reduced to a small anterior part and the cephalic vesicle has been completely reduced. Thus the large cavity at the anterior end of the Oncholaimidae is predominantly an onchial cavity and it must even be considered doubtful if any representative of the buccal cavity remains.

I interpret this type of head as a modification of the Enoplidae head in which the onchial cavity has come to dominate to the exclusion of all—or most—of the other components, as is argued by Filipjev (1934). Similarly the head in the Enchilidiidae can be interpreted as derived from the Enoplidae, although I am not sure about the relationships between the members of the Eurystominae and Enchilidiinae which look rather similar but are probably derived from very different sources.

The superfamily Tripyloidea of Chitwood (1950) and of Clark (1961) just cannot stand. The only character when Clark's classification is considered, which separates this group from the Enoploidea is " Cuticle of head not duplicate " particularly as his definition of the Enoploidea is " Cuticle of head duplicate : males with 0, 1 or 2 supplements ". This superfamily appears to have been a dumping ground for many diverse difficult groups and since I have discovered the presence of a cephalic capsule and a cephalic slit in *Trissonchulus* (see Inglis, 1961) and in *Thalassironus* (present paper) the resemblances of the Ironidae to the Enoploidea become overwhelming. The form of the male tail and the structure of the head and anterior end of the oesophagus suggests affinities with some of the Leptosomatidae. The taxonomic treatment of these groups is considered below.

As a consequence of what I argue above there is a sequence in mouth form running: three-lobed—six-lobed—three large lips—six-lobed or no lobes (Enchilidiidae, ? *Rhabdodemania*). Now Chitwood (1950) and de Coninck (1942) argue that the primitive mouth condition in the Nematoda is with six lips and they attempt to derive all other forms from this. I have already (Inglis, 1962) argued against this and shown that in the Subuluridae (Inglis, 1960) lip-lobes have appeared independently along at least three, and possibly four, evolutionary lines. Two principles were set out before, one—that as the mouth increases in size (that is, becomes more " open ") there is an associated development of, or increase in the size and efficiency of, a triturating mechanism ; and two—as the mouth opening increases in size the form taken by the bounding structures—lips—is determined by the mechanical requirements imposed by the cylindrical form of the body. This means that if the mouth opening is terminal—two dimensional (see above, page 274)—and the mouth is large it is most efficiently and strongly closed by a series of lip-lobes, usually six, while if it is closed by three they are most efficient when the mouth opening extends posteriorly to become three-dimensional so that bending of the lips takes place more posteriorly. The same functional requirements appear to have been met in the Enoplida. The primitive three-lobed mouth opening of forms such as *Anticoma* (even here there is an incipient division into six lobes) and *Crenopharynx* simply reflect the form of the oesophageal lumen posterior to them and their evolutionary modification with the appearance of a buccal cavity is discussed above (page 290) but when the mouth becomes large, as in the Enoplidae and Leptosomatidae it either extends posteriorly—as in the first family—or the lip structures are reduced to simple flaps of cuticle, as in the second family. The presence of six lip-lobes in the Oncholaimidae cannot on this basis be treated as a primitive condition but represents a modification to meet the functional demands imposed by the design of the body.

Thus the lip-lobes in forms such as *Pontonema* are not homologous with those of forms such as *Subulura ortleppi* Inglis, 1960 or *Allodapa baylisi* (Lòpez-Neyra, 1946) nor are three massive lips such as occur in the family Heterakidae (Inglis, 1957) and in the Ascaridoidea (Hartwich, 1952) homologous with the similar structures in the Enoplidae. I would argue that the so-called lips throughout the Nematoda are the expression of an evolutionarily plastic organ system reacting to similar functional demands in similar ways and that they have appeared and disappeared again and again along many different lines of evolutionary modification. This is most clearly established when the head is treated as a unit and Chitwood's (1950) errors in attempting to establish the homology of " lips " throughout the entire group have partly arisen from his methodology which is reflected by the separate treatment of " Cephalic Structures " and " Stoma ". That the form of the mouth opening, its bounding structures and the type of oesophageal modification are linked as a functional unit is now absolutely clear and is most spectacularly demonstrated by the conditions in the Enoplidae in which the head, in spite of its morphological complexity, reduces to what is virtually one taxonomic character. This subject will be discussed more fully and generally elsewhere as it involves a consideration of the concepts of homology which I do not wish to go into here.

DEFINITIONS OF MORPHOLOGICAL TERMS

The following terms have all been employed above and are listed here, with their definitions, for convenience. The page on which they are first employed is given in parentheses together with the number of a figure in which the structure is illustrated.

Buccal cavity—that part of the lumen of the digestive tract, anterior to the end of the oesophagus, which leads to the mouth opening (page 271; Text-figs. 1 and 2)

Buccal rods—rods of dense material developed in the inner layers of the cuticle lining the buccal cavity which are associated with the nerves to the labial sense organs (page 271 ; Text-fig. 1).

Cephalic capsule—a zone at the anterior end of the body in which the inner layer of the cuticle is thick and dense (page 269 ; Text-figs. 1 and 2).

Cephalic ring—a transverse ring of dense cuticle at the anterior edge of the cephalic capsule (page 271 ; Text-figs. 1 and 2).

Cephalic slits—supplementary sense organs on the ventro-lateral aspect of the head in the families Enoplidae and Ironidae (page 273 ; Text-fig. 77).

Cephalic ventricle—the fluid filled space which occupies the body anterior to oesophagus (page 271 ; Text-fig. 1).

Cervical capsule—a zone of longitudinally striated or punctate cuticle lying posterior to the cephalic capsule in some species of Phanodermatidae and Enoplidae (page 272 ; Text-fig. 86).

Cirrus—a long club-shaped projecting modification of the cephalic slits (page 273 ; Text-fig. 59).

Fenestrae—large, generally circular, expansions of the incisions from which arise the cephalic sense organs (page 269 ; Text-fig. 1).

Incisions—strips of clear cuticle running anteriorly from the posterior edge of the cephalic capsule which correspond to the position of the nerves which supply the cephalic sense organs (page 269 ; Text-fig. 1).

Mandible—a supporting and/or gripping organ developed in the inner layers of the cuticle lining the median part of the buccal cavity in the Enoplidae (page 275 ; Text-fig. 3).

Mandibular plate—a zone of dense cuticle lying between the mandibular rods (page 278 ; Text-fig. 72).

Mandibular ring—the most posterior, radially extended thin ring of specialized cuticle associated with the mandibles (page 276 ; Text-fig. 30).

Mandibular rods—lateral components of the mandibles which are probably homologous with buccal rods (page 278 ; Text-fig. 72).

Odontium—a tooth-like structure developed from the lining of the buccal cavity (page 271 ; Text-fig. 171).

Oesophageal capsule—a zone of thickened cuticle capping the anterior end of the oesophagus (page 269 ; Text-fig. 1).

Onchium—a tooth-like structure developed from the anterior end of oesophagus (page 271 ; Text-fig. 2).

Onchial cavity—an expansion of the lumen of the anterior end of the oesophagus within which the onchia originate (plate 275 ; Text-fig. 2).

Onchial plate—the dense thickened cuticle lining the onchial cavity, in association with the origins of the onchi, on to which is inserted the specialized musculature at the anterior end of the oesophagus in the Enoplidae (page 276 ; Text-figs. 5–7).

Radial masses—dense blocks of material which develop within the oesophagus, at its anterior end, opposite the ends of the radii of the oesophageal lumen in the Enoplidae (page 277 ; Text-fig. 25).

Radial processes—narrow strips of dense cuticle running, in conjunction with the mandibular ring, from the onchial plate to the radial masses (page 277 ; Text-figs. 5–7).

Semi-lunar striations—striations on the lining of the buccal cavity covering a zone bounded posteriorly by the mandibular ring and anteriorly by a curved line running from the projecting tip of the mandible to the inter-labial space (page 275 ; Text-fig. 61).

SYSTEMATIC SECTION

RELATIONSHIPS WITHIN THE MARINE ENOPLIDA

The classification at present in use for the marine members of the Enoplida is still predominantly that of Filipjev (1927), a report which is still the best available on this group of nematodes. Wieser's (1953) publication is of the greatest value to anyone studying the group but his interests were different from those of Filipjev and few changes are made in the classification. Clark's (1961) classification is largely useful as a list of all the genera which are generally referred to the Order, although he has over-looked a few, for example in the Enoplidae (Enoplinae of Clark) : *Thoracostomopsis* Ditlevsen, 1919 and *Trileptium* Cobb, 1933, should be added ; in the Leptosomatidae (-inae) : *Paraleptosomatides* Mawson, 1956 and three subgenera of *Thoracostoma—Pseudocella* Filipjev, 1927 ; *Corythostoma* and *Synonchoides* Wieser, 1956 should be added ; *Wieseria* Gerlach, 1956 should be added to the Oxystomidae (-inae), *Curvolaimus* Wieser, 1953 to the Oncholaimidae and *Gerlachystomina* Inglis, 1962 to the Eurystominae.

The Enoplida form a homogeneous group, which is also one of the most, if not the most, successful, of the Nematoda. The classification of at least the marine members is at present clearly unsatisfactory since it is artificial and does not reflect the phylogenetic interrelationships of the groups concerned. One major factor in the appearance of the group was the development of the attachment of the oesophagus to the outer wall of the body so that to use the presence or absence of a cephalic capsule or the presence or absence of the cephalic ventricle as a character is likely to lead to error since it could easily have, and almost certainly has, been lost along more than one evolutionary line. I am sure that originally such an attachment existed in all root stocks of the Enoplida and its absence in some forms is almost certainly due to its later loss not to it never having existed in an ancestral form. Within the marine members of the order, which are almost all referred to the Suborder Enoplina by Clark (1961), there appear to be at least two major evolutionary lines which do not correspond to the classification advanced by Filipjev, Chitwood or Clark. The division of the suborder into two Superfamilies Enoploidea and Tripyloidea cannot stand. The latter superfamily as constituted by Chitwood (1950) contains a heterogenous group of genera from which Thorne (1939) removes the Alaimidae to the Dorylaimoidea. Clark (1961) removes the Mononchidae to the Dorylaimoidea and, creates a new Suborder Alaimina for the Alaimidae. As a result the superfamily Tripyloidea of Clark contains only two families, Trypylidae and Ironidae, of which the Ironidae form a remarkably uniform group characterized by a slight cephalic capsule and prominent solid onchia, the cephalic vesicle is lost, the buccal cavity is small, there is, in at least two genera—*Trissonchulus* and *Thalassironus*—a cephalic slit and the oesophageal glands empty near the anterior end of the oesophagus. All this demonstrates close relationship to the Enoploidea of Chitwood and Clark.

The Tripylidae which contains two genera, *Tripyla* Bastian, 1865 and *Tobrilus* Andrássy, 1959 is restricted to forms occurring in soil and freshwater and falls outside the limits of my discussion. It should, however, be pointed out that its relationships to other Enoplida are not clear and De Coninck (1935) includes *Tripyla* in the family Bastianidae of the Axonolaimida. Chitwood (1950) refers the Tripylidae to the Enoplida and the Bastianidae as an appendix to the Plectoidea. The relationships of this group are clearly uncertain. The same may be said of the Cryptonchinae Chitwood, 1937 which contains only one genus, *Cryptonchus* Cobb, 1913. This also is a freshwater group of uncertain relationships.

The Enoploidea, according to Clark, contains three families : Enoplidae, with four subfamilies, Enoplinae, Leptosomatinae, Phanodermatinae and Oxystominae ; Lauratonematidae, with no subfamilies and only one genus—*Lauratonema* Gerlach, 1953 and Oncholaimidae, with three subfamilies, Oncholaiminae, Eurystominae and

Enchilidiinae. This division appears to reflect convergent similarities rather than phylogenetic relationships. I would argue that a simple head form without a cephalic ventricle or any odontia or onchia is primitive to the Order. This is in agreement with the arguments of Filipjev (1934) who suggests " The Leptosomatidae are the simplest forms ". As Filipjev also points out, the most primitive Oxystomatinae " are very similar to the Leptosomatidae " and the " Phanodermatinae in its simplest members, ... , closely resembles the Leptosomatinae as regards the structure of the head ". Chitwood (1950) argues in the opposite way " In the Enoplidae stomata are definitely on the wane, being rudimentary in the Oxystomatininae and Phanodermatinae, represented chiefly by three mandibles in the Enoplinae and usually quite inconspicuous in the Leptosomatinae " and " Filipjev (1934) considered enoploids such as *Leptosomatum* which have no definite clear cut stoma as the more primitive while the writers regard forms such as *Rhabditis* and *Plectus* with distinct elongated stomata as primitive " and " Undoubtedly the Tripyloidea is the most primitive group of the order Enoplida, and hence most closely related to the Plectoidea. . . ." With all this I disagree strongly and am in complete agreement with Filipjev on the form of the most primitive heads.

The head in the Enoplidae is characterized by a complex of functionally interdependent characters which I have argued can be derived from the much simpler head forms found in the Phanodermatidae. In this I disagree with Filipjev (1934) who derives the Enoplinae from the Leptosomatinae by way of *Triodontolaimus*. The simplest forms in the Phanodermatidae approach the theoretical primitive head form and these two families appear to represent a natural group within which there are probably several evolutionary lines but the analysis of any such lines is not at present possible. There is a possibility that genera such as *Oxyonchus*, *Savaljevia* and *Parasavaljevia* represent an elaboration of the Phanoderma-type head which has developed independently of the other genera usually referred to the Enoplidae while *Enoplus* can be considered to represent the extreme in the development of the mandibular component of the head to the almost complete exclusion of the onchial along a (?) separate line including *Enoploides*, *Metenoploides* and, possibly, *Parenoplus*. The great difficulty in analysing this is the unsatisfactory grouping of species in the genera *Enoplolaimus*, *Mesacanthion*, *Enoploides* and *Paramesacanthion* (see page 310 for more detailed discussion) and until this can be unravelled the position must remain most unsatisfactory.

I consider the Oncholaimidae to be a group derived from the same broad Phanodermatidae: Enoplidae line which has radiated by the great expansion of the onchial component of the head with the almost complete suppression of the mandibular. Thus I interpret the large cavity of the Oncholaimidae as representing a great expansion of the onchial plate component of the Enoplidae. The Eurystominae and Enchilidiinae probably derived from the same line but they do not appear to be closely related to the Oncholaimidae. It is not clear how far they are themselves related since they probably represent the end results of massive convergence. The genus *Rhabdodemania*, which is a rather peculiar group of species, is probably nearer the Eursytominae: Enchilidiinae groups than it is to any other and could represent an ancestral type from which one of these subfamilies has been derived. It is, however, too specialised to give more than a hint in this direction and I shall continue to treat it here as a member of the Enoplidae.

The Leptosomatidae are clearly on a different evolutionary line from those discussed above. The form of the head is totally different with the oesophageal musculature passing far anteriorly and the buccal cavity developing, in the more advanced forms, a series of cuticular odontia. In this line also the simplest head forms are without buccal cavities or cephalic vesicles and the attachment of the oesophagus to the body wall is over a wide cap-like area at the anterior end. The specialization of the head appears to have prevented any massive change in the level of organization such as appears to characterize the derivation of the Oncholaimidae from the Enoplidae/Phanodermatidae line. Nevertheless it is possible that the Ironidae have been derived from this line in view of the similarities in the modification of the anterior end of the oesophagus, the form of the male tail and of the spicules. The position of this family must remain uncertain since the head could also—although I think less probably—have been derived from a form similar to that of the Enoplidae. I can make no observations on the Oxystomidae as I have not studied any members of this family but they appear to be somewhat similar to, and should later probably be classified with, the Leptosomatidae.

The general conclusions I draw are: 1—the Phanodermatidae/Enoplidae/Oncholaimidae form a related group, with the Eurystominae and Enchilidiinae probably derived from them. I would not, however, treat the latter subfamilies in the same family as the Oncholaimidae since I am sure their similarities are those of convergence. 2—the Oxystomidae : Leptosomatidae : Ironidae probably form a second related group. I am not prepared to advance any formal classification based on these ideas until I have had an opportunity to study more specimens, particularly of the Oxystomidae and Leptosomatidae. I shall therefore simply refer to the following families, Phanodermatidae, Enoplidae, Leptosomatidae, Enchilidiidae, Oncholaimidae and Ironidae.

LIST OF SPECIES DESCRIBED

The study reported above was based on specimens collected from South African waters among which are representatives of twenty four species, of which twenty two are described as new, belonging to eighteen genera, of which four are new, thus :

Phanodermatidae

Dayellus gen. nov. (page 304).
    Dayellus dayi sp. nov. (page 304).
Crenopharynx Filipjev, 1934 (page 306).
    Crenopharynx eina sp. nov. (page 306).
    Crenopharynx afra sp. nov. (page 308).
Phanoderma Bastian, 1865 (page 309).
    Phanoderma unica sp. nov. (page 309).

Enoplidae

- *Oxyonchus* Filipjev, 1927 (page 311).
  - *Oxyonchus ditlevseni* sp. nov. (page 311).
- *Enoplolaimus* de Man, 1893 (page 312).
  - *Enoplolaimus mus* sp. nov. (page 312).
- *Mesacanthion* Filipjev, 1927 (page 313).
  - *Mesacanthion cavei* sp. nov. (page 313).
  - *Mesacanthion ceeus* sp. nov. (page 314).
  - *Mesacanthion studiosa* sp. nov. (page 315).
- *Africanthion* gen. nov. (page 316).
  - *Africanthion nudus* sp. nov. (page 316).
- *Trileptium* Cobb, 1933 (page 317).
  - *Trileptium ayum* sp. nov. (page 317).
- *Thoracostomopsis* Ditlevsen, 1919 (page 318).
  - *Thoracostomopsis carolae* sp. nov. (page 319).
- *Enoplus* Dujardin, 1845 (page 320).
  - *Enoplus harlockae* sp. nov. (page 320).
  - *Enoplus michaelseni* Linstow, 1896 (page 321).
- *Rhabdodemania* Baylis and Daubney, 1926 (page 322).
  - *Rhabdodemania nancyae* sp. nov. (page 322).

Leptosomatidae

- *Anticoma* Bastian, 1865 (page 324).
  - *Anticoma chitwoodi* sp. nov. (page 324).
- *Parabarbonema* gen. nov. (page 326).
  - *Parabarbonema barba* sp. nov. (page 326).
- *Macronchus* gen. nov. (page 328).
  - *Macronchus shealsi* sp. nov. (page 328).
- *Thoracostoma* Marion, 1870 (page 330).
  - *Thoracostoma angustifissulatum* Mawson, 1956 (page 331).
  - *Thoracostoma jae* sp. nov. (page 332).
  - *Thoracostoma zeae* sp. nov. (page 334).

Enchilidiidae

- *Eurystomina* Filipjev, 1918 (page 335).
  - *Eurystomina sudensis* sp. nov. (page 335).

Oncholaimidae

- *Pontonema* Leidy, 1856 (page 336).
  - *Pontonema yaena* sp. nov. (page 336).

Ironidae

- *Thalassironus* de Man, 1889 (page 337).
  - *Thalassironus jungi* sp. nov. (page 337).

SPECIES PRESENT IN EACH SAMPLE

The specimens studied were collected by hand from grab or trawl samples from a large number of localities. Unfortunately in many cases the material is so very badly preserved that it is impossible to study the specimens collected. Thus the numbers and distribution of the specimens and species can give little more than some vague indication of the populations sampled and the distribution and habitat preferences of the species present. The following list refers only to the samples studied during the taxonomic study and does not include any which were in poor condition. Details of the stations and of the Ecological Survey are given by Day (1961). The small number of species referable to orders other than Enoplida was described elsewhere (Inglis, 1963). The holotypes and some paratypes of all new species are deposited in the British Museum (Natural History) indicated by B.M. (N.H.) Reg. Nos. Representative specimens of each species, where possible, have been returned to the University of Cape Town.

False Bay Dredging (FAL)

FAL.392. 34° 12·6′ S/18° 29·1′ E. Khaki mud from 40 metres on 15.11.60.
Dayellus dayi (5♂♂, 3♀♀, 2 larvae).
FAL.408. 34° 08.8′S/18° 33·5′ E. Khaki coloured sand from 32 metres on 16.5.61.
Dayellus dayi (1♂, 1♀).

South Coast Dredging (SCD)

SCD.212. 33° 58·8′ S./ 25°42·2′ E. Coarse sand, broken shells from 26 metres on 24.11.60.
Crenopharynx eina (1♂, 3 larvae).
Mesacanthion cavei (1♂, 1 larva).
Mesacanthion ceeus (1♂).
Trileptium ayum (1♂, 1♀, 1 larva).
Rhabdodemania nancyae (10♂♂, 10♀♀).
SCD.220. 34° 02′ S./23° 48·4′ E. Sand, mud and rock from 50 metres on 29.11.60.
Dayellus dayi (2♂♂).
Anticoma chitwoodi (2♂♂, 1 larva).
SCD.233. 36° 28·5′ S./21° 11·0′ E. Khaki coloured sand from 182 metres on 4.12.60.
Crenopharynx afra (1♂, 1♀).

West Coast Dredging (WCD)

WCD.90. 32° 05′ S./18° 17′ E. Coarse white sand from 39 metres on 2.7.61.
Enoplolaimus mus (1♂, 1♀, 1 larva).
Africanthion nudus (6♀, 2 larvae).
Thoracostomopsis carolae (2♂♂, 1♀, 2 larvae).
Parabarbonema barba (12♂♂, 17♀♀, 29 larvae).
Macronchus shealsi (13♂♂, 11♀♀, 9 larvae).

WCD.91. 32° 02′ S./18° 17′ E. Coarse white sand from 27 metres on 2.7.61.
Enoplolaimus mus (15♂♂, 19 larvae).
Mesacanthion cavei (1♂).
Mesacanthion studiosa (1♂).
Trileptium ayum (1♀).
Macronchus shealsi (1 larva).
Pontonema yaenae (10♂♂, 5♀♀, 3 larvae).

WCD.93. 32° 05′ S./18° 17′ E. Coarse white sand from 39 metres on 2.7.61.
Phanoderma unica (1♂).
Africanthion nudus (2♂♂, 4♀♀, 1 larva).
Thoracostomopsis carolae (1♀).
Parabarbonema barba (6♂♂, 3♀♀, 3 larvae).
Rhabdodemania nancyae (3♂♂, 5♀♀, 4 larvae).
Macronchus shealsi (15♂♂, 18♀♀, 22 larvae).
Thalassironus jungi (2♂♂, 1♀).

WCD.94. 32° 05′ S./18° 16′ E. Khaki coloured mud from 54 metres on 2.7.61.
Oxyonchus ditlevseni (1♂).
Enoplolaimus mus (1♂, 2♀♀).
Thoracostomopsis carolae (1♂, 2♀♀).
Parabarbonema barba (3♂♂).
Macronchus shealsi (11♂♂, 12♀♀, 8 larvae).
Eurystomina sudensis (2♂♂, 1♀).
Rhabdodemania nancyae (6♂♂, 8♀♀, 3 larvae).
Thalassironus jungi (3♂♂, 11♀♀, 5 larvae).

WCD.99. 32° 16′ S./18° 17′ E. Coarse white sand from 27 metres on 2.7.61.
Enoplolaimus mus (1♀, 2 larvae).
Mesacanthion studiosa (2♂♂, 2♀♀, 2 larvae).
Enoplus harlockae (1♂).
Enoplus michaelseni (1♂, 1 larva).
Thoracostoma angustifissulatum (1♂).
Thoracostoma jae (6♂♂, 5♀♀, 5 larvae).
Thoracostoma zeae (1♂, 3 larvae).
Pontonema yaenae (4♂♂, 3♀♀, 2 larvae).

WCD.102. 32° 05′ S./18° 16′ E. Khaki mud from 54 metres on 2.7.61.
Macronchus shealsi (5♂♂).

DESCRIPTIVE SECTION

Family **PHANODERMATIDAE** Filipjev, 1927

Currently eight genera, the limits of which are in many cases most uncertain, are referred to this family. I do not intend to discuss them here but I would point out that although the majority are considered to differ in the structure of the head most of the available descriptions are quite insufficient to allow its form to be established. This difficulty has become most pressing in relation to the new genus, *Dayellus*, which I erect below. The presence of buccal rods or their pre-cursors has now been established in three genera, *Phanoderma*, *Crenopharynx* and *Dayellus*, and it appears probable that this is a common character throughout the family which may be diagnosed thus :

> Enoplida : oesophagus "cellular"; mandibles never present ; cephalic capsule and cephalic vesicle not massive ; pre-cloacal supplement(s) usually tuboid. Type genus : *Phanoderma* Bastian, 1865.

Four species, belonging to three genera, referable to this family are present in the collections, thus :

DAYELLUS gen. nov.

Dayellus dayi gen. et sp. nov.

(Text-figs. 38–42)

MATERIAL STUDIED. 5 ♂♂ (1 selected as holotype), 3 ♀♀, 2 larvae (1 late 4th-stage). 34° 12·6′ S./18° 29·1′ E. on 15.11.60 from khaki mud at a depth of 40 metres (FAL 392). B.M. (N.H.), Reg. Nos. 1963. 184–193.

1 ♂, 1 ♀. 34° 08·8′ S./18° 33·5′ E. on 16.5.61 from fine khaki coloured sand at a depth of 32 metres (FAL 408). B.M. (N.H.), Reg. Nos. 1963. 194–195.

2 ♂♂. 34° 0·2′ S./23° 48·4′ E. on 29.11.60 from sand, mud and rock at a depth of 50 metres. SCD 220 (returned to Cape Town).

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	63·6	5·8	19·4		6·8
	59·2	6·0	20·8		7·7
	65·0	6·2	23·6		7·8
	60·7	6·3	23·0		8·5
	74·6	6·6	24·8		9·7
Females	65·4	7·0	25·0	44·7	8·5
	62·1	6·7	24·7	45·6	8·7
	64·3	6·9	25·0	44·4	9·0
Larvae	69·0	6·8	21·6		6·9
	67·3	6·2	23·9	52·7	7·4 (4th-stage)

MEASUREMENTS (in mm. in order of body lengths). *Male.* Body breadth : 0·11 ; 0·13 ; 0·12 ; 0·14 ; 0·13. Oesophageal length : 1·18 ; 1·28 ; 1·25 ; 1·35 ; 1·46. Diameter of head : 0·010 ; 0·011 ; 0·009 ; 0·011 ; 0·012. Diameter of cephalic capsule at posterior edge : 0·016 ; 0·017 ; 0·013 ; 0·017 ; 0·018. Depth of cephalic capsule : 0·009 ; 0·009 ; 0·008 ; 0·009 ; 0·010. Length of cephalic setae : 0·022 and 0·019 ; 0·022 and 0·019 ; 0·022 and 0·020 ; 0·021 and 0·017 ; broken. Distance of nerve ring from anterior end : 0·327 ; 0·336 ; 0·331 ; 0·339 ; 0·366. Distance of excretory pore from anterior end : 0·069 ; 0·078 ; 0·074 ; 0·080 ; 0·081. Tail length : 0·35 ; 0·37 ; 0·33 ; 0·37 ; 0·39. Cloacal diameter : 0·064 ; 0·067 ; 0·075 ; 0·081 ; 0·084. Length of spicules : 0·126 ; 0·131 ; 0·135 ; 0·144 ; 0·135. Length of gubernaculum : 0·048 ; 0·050 ; 0·049 ; 0·051 ;

0·051. Length of pre-cloacal supplement : 0·027 ; 0·029 ; 0·026 ; 0·027 ; 0·028. Distance of pre-cloacal supplement anterior to cloacal opening : 0·042 ; 0·045 ; 0·045 ; 0·045 ; 0·048.

Female. Body breadth : 0·13 ; 0·14 ; 0·14. Oesophageal length : 1·28 ; 1·30 ; 1·30. Diameter of head : 0·011 ; 0·009 ; 0·010. Diameter of cephalic capsule at posterior edge : 0·017 ; 0·015 ; 0·016. Depth of cephalic capsule : 0·010 ; 0·010 ; 0·010. Length of cephalic setae : 0·025 and 0·022 ; 0·025 and 0·022 ; 0·026 and 0·023. Distance of nerve ring from anterior end : 0·387 ; 0·354 ; 0·356. Distance of excretory pore from anterior end : 0·074 ; 0·073 ; 0·071. Tail length : 0·34 ; 0·36 ; 0·36. Anal diameter : 0·081 ; 0·073 ; 0·075. Distance of vulva from anterior end : 3·8 ; 4·1 ; 4·0.

Larvae. Body breadth : 0·10 ; 0·11. Oesophageal length : 1·02 ; 1·25. Diameter of head : 0·099 ; 0·010. Diameter of cephalic capsule at posterior edge : 0·014 ; 0·015. Depth of cephalic capsule : 0·008 ; 0·008. Length of cephalic setae : 0·018 and 0·016 ; 0·018 and 0·017. Distance of nerve ring from anterior end : 0·324 ; 0·312. Distance of excretory pore from anterior end : 0·072 ; 0·063. Tail length : 0·32 ; 0·31. Anal diameter : 0·063 ; 0·075. Distance of vulva from anterior end in second larva : 3·9.

The head is similar to that of *Phanoderma* in possessing both a stomodaeal and a cephalic capsule, a mouth opening bounded by six indistinct lip-lobes, which are supported by the buccal rods, a triangular buccal cavity in cross section and an outer circle of ten long cephalic setae of which six are long and four are short. The anterior end of the body is, in many of the specimens, set-off by a constriction which appears to coincide with the posterior edge of the cephalic capsule. This constriction may be an artefact as it is not present in all the specimens. Due to the poorish condition of the specimens the exact outline of the capsules cannot be wholly established but the stomadaeal capsule definitely enfolds the lateral setae as shown in Text-fig. 38 while the cephalic capsule is straight posteriorly and terminates posterior to the cephalic setae (Text-figs. 38 and 41). The anterior end of the oesophagus is simple and has the typical cellular appearance posteriorly.

The tail terminates in a narrow flagellate portion in both sexes. In the male the spicules are equal in length and identical in structure. They are short with bluntly capitate posterior ends and are without alae. The gubernaculum is fairly massive with a pair of stout, bluntly rounded apophyses and a pair of thin, lightly built, lateral rods which project laterally and anteriorly (Text-figs. 40 and 42). There is a single, simple, rod-like pre-cloacal supplement which lies a relatively short distance anterior to the cloacal opening. Possibly because of the condition of the specimens no setae have been seen on the tail. The caudal glands lie posterior to the cloacal opening and there appear to be two opposed testes. The sperm are flagellate.

The female reproductive system is double with reflexed ovaries which lead into relatively large uteri which appear to be modified distally as spermathecae. The eggs are large and elongate, 0·20 × 0·099 mm. and 0·23 × 0·090 mm. being typical examples.

DISCUSSION

This species does not appear to be congeneric with any others referred to the family Phanodermatidae. It probably approaches the genus *Phanodermella* Kreis, 1928 most closely but differs from it in the form of the gubernaculum and (?) the structure of the head. The new genus, *Dayellus*, may be diagnosed thus :

> Phanodermatidae : mouth opening surrounded by six-lobes supported by six buccal rods ; cephalic vesicle prominent ; no onchia are present ; cephalic capsule simple ; both cephalic and oesophageal capsules small ; cephalic setae relatively long.
>
> Male. Spicules short ; pre-cloacal supplement present ; gubernaculum with a massive dorsal apophysis.
>
> TYPE SPECIES : *Dayellus dayi* sp. nov.

Crenopharynx Filipjev, 1934

The systematic relationships of this genus are discussed by Schuurmans Stekhoven (1950) and Allgén (1932) who conclude that it shows similarities with the Leptosomatidae rather than the Phanodermatidae where it is placed by Filipjev (1934). With this suggestion Wieser (1953) disagrees, arguing with Filipjev that it should be included in the Phanodermatidae, an argument which I fully accept. Schuurmans Stekhoven compares it with *Anticoma* and argues that the two genera should be within the same family. However, I would interpret the points of similarity as relatively primitive characters and argue that the two genera have them in common because they are both somewhat primitive in structure. *Crenopharynx* clearly belongs with the Phanodermatidae because of the cellular form of the oesophagus and also the form of the head, while *Anticoma* (see page 324) for similar reasons should be referred to the Leptosomatidae.

The genus *Crenopharynx* may be diagnosed thus :

> Phanodermatidae : mouth opening tri-radiate ; incipient buccal rods present ; prominent muscular onchia (?) present ; buccal cavity fits close to onchia ; cephalic vesicle small ; cephalic capsule lightly built ; oesophageal capsule not seen.
>
> MALE : spicules long, narrowing rapidly towards the distal end ; barb usually developed at point where spicule narrows ; gubernaculum small and close lying.
>
> TYPE SPECIES : *Anoplostoma gracile* Linstow, 1900.

Crenopharynx eina sp. nov.

(Text-figs. 43–44, 47–49)

MATERIAL STUDIED. 1 ♂ (holotype) ; 3 larvae. 33° 58·8′ S./25° 42·2′ E. on 24.11.60 from sand and broken shells from a depth of 26 metres (SCD 212). B.M. (N.H.), Reg. Nos. 272–275.

	Ratios			
	a	*b*	*c*	*Body Length (mm.)*
Male	29·1	4·3	18·9	6·4
Larvae	31·4	3·4	13·8	4·4
	26·8	3·9	16·2	5·1
	32·2	4·1	17·7	5·8

MEASUREMENTS (in mm. in order of body lengths). Body breadth : 0·22 ; 0·14 ; 0·19 ; 0·18. Oesophageal length : 1·49 ; 1·28 ; 1·31 ; 1·42. Diameter of head : 0·019 ; 0·016 ; 0·013 ; 0·017. Diameter of cephalic capsule at posterior edge : 0·026 ; 0·021 ; 0·022 ; 0·023. Depth of cephalic capsule : 0·012 ; 0·011 ; 0·011 ; 0·012. Length of cephalic setae : 0·013 and 0·018 ; 0·014 and 0·016 ; 0·010 and 0·014 ; 0·013 and 0·017. Distance of nerve ring from anterior end : 0·56 ; 0·54 ; 0·55 ; 0·58. Distance of excretory pore from anterior end : 0·18 ; 0·14 ; 0·16 ; 0·15. Tail length : 0·339 ; 0·318 ; 0·315 ; 0·328. Cloacal or anal diameter : 0·110 ; 0·084 ; 0·099 ; 0·099. Length of spicules : 0·463. Length of gubernaculum : 0·074.

The head is small and blunt (Text-fig. 49) and the oesophagus is typical, thin anteriorly and cellular posteriorly. The tail is relatively short and stoutish (Text-fig. 47) with the caudal glands lying posterior to the cloacal opening.

The spicules are equal in length and identical in structure. They are long and thin, expanding very slightly just anterior to the point at which they suddenly narrow very markedly to terminate in the long narrow tip which is apparently a diagnostic character of the genus (Text-fig. 47). Just at the point where they narrow is a small, but distinct, sharp pointed barb which is directed towards the distal end of the spicule. The gubernaculum is rather large with distinct lateral processes at the distal end (Text-fig. 48). There are two opposed testes.

DISCUSSION

The genus *Crenopharynx* currently contains six species, *C. gracilis* (Linstow, 1900) type species, *C. brevicaudatus* (Schuurmans Stekhoven, 1950), *C. crassus* (Ditlevsen, 1930), *C. marioni* (Southern, 1914), *C. metagracilis* (Schuurmans Stekhoven, 1950) and *C. paraleptus* (Schuurmans Stekhoven, 1950) of which *C. brevicaudatus* (not *C. brevicauda* as mis-spelt by Wieser, 1953) and *C. metagracilis* are insufficiently known for any comparison to be possible (they should probably be dismissed as *species dubia*). From the remaining species *C. eina* may be distinguished, apparently, by the presence of a distinct barb on the spicules although the description of *C. paralepturus* is insufficient to establish this. However, *C. eina* differs from that species, as well as all the others, in the shortness of the tail. It also differs from *C. marioni*, *C. crassus* and *C. gracilis* in the presence of lateral processes on the gubernaculum.

Crenopharynx eina is characterized by a relatively short tail, a barb on each spicule just anterior to the narrow terminal zone and the presence of lateral processes to the gubernaculum.

Crenopharynx afra sp. nov.

(Text-figs. 45–46)

MATERIAL STUDIED. 1 ♂ (holotype), 1 ♀. On 4.12.60 from khaki coloured sand from 182 metres at 36° 28·5′ S./21° 11′ E. (SCD 233). B.M. (N.H.), Reg. Nos. 1961. 276–277.

Ratios

	a	*b*	*c*	*V*	*Body Length (mm.)*
Male	53·1	3·3	14·7		6·9
Female	43·7	4·2	13·8	67·5	8·3

MEASUREMENTS (in mm., Male first, then Female). Body breadth : 0·13 ; 0·19. Oesophageal length : 2·10 ; 1·98. Diameter of head : 0·022 ; 0·023. Diameter of cephalic capsule at posterior edge : 0·030 ; 0·031. Depth of cephalic capsule : 0·017 ; 0·016. Length of cephalic setae : 0·010 and 0·011 ; 0·010 and 0·012. Distance of nerve ring from anterior end : 0·64 ; 0·68. Distance of excretory pore from anterior end : 0·18 ; 0·19. Tail length : 0·47 ; 0·60. Cloacal or anal diameter : 0·11 ; 0·14. Length of spicules : 0·447. Length of gubernaculum : 0·113. Distance of vulva from anterior end : 5·6.

This species is similar to the previous species in general structure. For example, the structure of the head and oesophagus, so far as can be determined, is exactly the same but it differs markedly in the shape of the tail which in this species terminates in a long flagellate portion (Text-fig. 45). The spicules, while having the same general shape, with a long narrow terminal portion, lack the distinct barb present in *C. eina*. This structure is here represented by a slight swelling of the spicules at approximately the same point along their lengths (Text-fig. 46). The form of the gubernaculum is also different. It is a rather slim structure which clings closely to the spicules, enclosing them along a good part of its length, and lacks the processes which are found in *C. eina* (Text-figs. 45 and 46). The eggs are 0·28 mm. × 0·19 mm.

DISCUSSION

This species is very similar to *C. crassus* (Ditlevsen, 1930) both in the shape of the tail and the shape of the gubernaculum. However, the form of the spicules cannot be established in Ditlevsen's species and I shall treat my specimens as, at least provisionally, distinct.

Crenopharynx afra is characterized by a long, flagellate tail, a lightly built gubernaculum with extensive lateral pieces and spicules without a definite barb near their posterior ends but having instead a slight swelling.

Phanoderma Bastian, 1865

Phanoderma unica sp. nov.

(Text-figs. 50–54)

MATERIAL STUDIED. 1 ♂ 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres. (WCD.93). B.M. (N.H.), Reg. No. 1963. 58.

Ratios

a	*b*	*c*	*Body Length (mm.)*
67·5	5·7	27·9	8·1

MEASUREMENTS (in mm.). Body breadth : 0·12. Oesophagus length : 1·43. Length of cephalic setae, long/short : 0·029/0·021. Cephalic capsule, length/diameter : 0·016/0·023. Distance of nerve ring from anterior end of body : 0·41. Distance of excretory pore from anterior end of body : 0·026. Distance of eye spots from anterior end of body : 0·054. Tail length : 0·29. Cloacal diameter : 0·093. Spicule length : 0·153. Gubernaculum length : 0·030. Distance of pre-cloacal supplement anterior to cloacal opening : 0·051.

No cervical capsule is present but eye spots are present. The structure of the head is typical (see above, page 271, and Inglis (1962)). The tail is fairly long, the spicules are short and stout without plates, the pre-cloacal supplement lies fairly close to the cloacal opening, the gubernaculum is complex with a massive double apophysis and the lateral pieces are developed as long embracing processes (Text-fig. 52). There is a median piece projecting between the spicules. Cephalic capsule very simple and straight posteriorly (Text-figs. 53 and 54).

DISCUSSION

This species appears to be distinct on the basis of the shape of the gubernaculum, the lack of a cervical capsule and the simplicity of the cephalic capsule but I am not happy about the present generic groupings within the Phanodermatidae. Many of the characters used appear to be those which could easily be over-looked or misinterpreted. Further, division of the genus *Phanoderma* on the basis of presence or absence of eye spots as is done by Wieser (1953) appears to be a division on a bibliographic rather than a biological character. The whole group is in drastic need of revision.

Family **ENOPLIDAE** Baird, 1853

This family represents a group of morphologically very similar genera and, probably because of their relatively great size, the structure of the various organ systems has been frequently studied. The major characters for the delimitation of genera have almost all come from the structure of the head. This, it has been shown above, forms a complex of interrelated and interdependent functional characters and it would, as a result, be liable to show considerable convergence in morphological structure. The major characters used in delimiting genera have been the form of the mandibles, the relative lengths of the onchia, the position of origin of the cephalic setae and, as a subsidiary character, the presence of striated lips. For a discussion of the value of various other characters, for example the form of the spicules, the gubernaculum, and the pre-cloacal supplement, see Filipjev (1927) whose comments on their minor value appear to be well founded. The diagnosis of the family is fairly straight forward although there are some marginal groups to which some of the characters do not apply, but in general the following combination of characters occurs :

> Enoplida : cephalic capsule and cephalic ring well developed ; cephalic ventricle prominent ; oesophageal musculature always stops posterior to cephalic and mandibular rings ; cephalic slit present ; three onchia usually present ; mandibular complex well developed ; buccal cavity usually well developed ; amphids not elongate ; oesophagus " cellular " due to restriction of musculature to distinct zones ; usually one tuboid pre-cloacal supplement.
>
> TYPE GENUS : *Enoplus* Dujardin, 1845.

The delimitation of genera within the family is extremely complicated in view of the forms taken by the mandibles. In particular I suspect that the position of the cephalic setae relative to the cephalic ring is not a reliable character and that this varies along more than one line. Further, it is clear that at least three types of mandibular complex occur among the species currently referred to *Enoplolaimus*, *Mesacanthion*, *Enoploides* and *Paramesacanthion* and that species with the same type of mandible have been classified in different genera. This is not to suggest that the form of the mandible in itself is a rigid character for the allocation of species but it does appear to be a good indication of the degree of development of the other structures in the cephalic complex and may be taken as some indication of the other conditions in the head. Thus, the type of mandible in *Enoplolaimus mus* which I describe below, in which the mandibular rods are separate from the mandibular plate over a large part of their lengths, appears to be different from that found in the type species of *Enoplolaimus*, *E. vulgaris* de Man, 1893. In this latter species the mandibular rods appear to be wholly attached to the mandibular plate to produce a mandible of the type I describe for *Africanthion*. The *E. mus* type of mandible appears to be present in, for example, *E. lenunculus* Wieser, 1959, *E. paralitoralis* Wieser, 1959, *E. oxycephalus* Ditlevsen, 1926 (referred to *Mesacanthion* by Filipjev (1927) and then to *Paramesacanthion* by Wieser (1953)), *E. virilis* Ditlevsen, 1930 (referred to *Mesacanthion* by Wieser (1953)), and *Mesacanthion klugei* Filipjev, 1927. The more massive type of fused mandible, similar to that of *Africanthion*, appears to occur in, for example, *Enoplolaimus distortus* Gerlach, 1957, *E. connexus* Wieser, 1953, *Mesacanthion rigens* Gerlach, 1957, *M. infantilis* of Wieser, 1953 non *Enoplolaimus infantilis* Ditlevsen, 1930, *M. lucifer* Filipjev, 1927, and *M. africanum* Gerlach, 1957a. The most massive type of mandible, such as I describe here for three new species of *Mesacanthion*, appears to occur, for example, in *Mesacanthion breviseta* Filipjev, 1927, *M. major* Filipjev, 1927, *Enoploides amphioxi* Filipjev, 1918, *E. hirsutus* Filipjev, 1918, *E. brevis* Filipjev, 1918 and several other species which have been referred to *Enoploides* by various authors. This listing is not intended to be exhaustive but only indicative of the scale of the problem to be resolved. It appears almost certain that the family Enoplidae as at present constituted contains several parallel lines of modification the members of which have been grouped on the basis of general morphological similarity rather than phylogenetically. A problem on this scale cannot be solved within the confines of a single report and I can only draw attention to it at this time. As a result the generic allocation of the species I describe below is based as far as possible on what appears to be the usual practice and largely on the generic groupings of Wieser (1953) which must for some time to come continue to supply the best practical basis for classification.

Oxyonchus Filipjev, 1927

This genus is characterized, particularly, by the presence of unequal onchia of which the longer ventro-lateral do not extend anterior to the anterior edge of the mandibular plate. It is morphologically very similar to *Savaljevia* Filipjev, 1927 and *Parasavaljevia* Wieser, 1953 but differs in the form of the mandibular complex and the length of the ventral onchia (see Wieser, (1953) for discussion). The genus may be diagnosed thus :

> Enoplidae : mandibular rods separate from mandibular plate ; dorsal onchium small ; ventro-lateral onchia equal and large but not extending beyond anterior edge of mandibular plate ; series of small denticles developed from inner surface of mandibular plate ; cephalic setae arising from near cephalic ring ; spicules short and stout ; gubernaculum with apophysis ; pre-cloacal supplement small.

TYPE SPECIES : *Enoplolaimus hamatus* Steiner, 1916.

Oxyonchus pachylabiatus Schuurmans Stekhoven, 1946 does not agree with this diagnosis since, according to Schuurmans Stekhoven, it lacks a supplement and an apophysis to the gubernaculum but his male specimen looks suspiciously like a 4th-stage larva.

Oxyonchus ditlevseni sp. nov.

(Text-figs. 55–59)

MATERIAL STUDIED. 1 ♂. 32° 05′ S./18° 16′ E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. No. 1963. 129.

Ratios

a	*b*	*c*	*Body Length (mm.)*
37·6	4·8	11·7	3·5

MEASUREMENTS (in mm.). Body breadth : 0·093. Oesophagus length : 0·73. Diameter of head : 0·033. Length of cephalic setae, long/short : 0·036/0·012. Tail length : 0·30. Cloacal diameter : 0·056. Spicule length : 0·060. Gubernaculum length : 0·033. Distance of pre-cloacal supplement anterior to cloacal opening : 0·127.

The head bears a well developed " cirrus " and the mandibles bear about sixteen small denticles arranged roughly in two rows. The cephalic setae are long and thin with six longer than the remaining four. There are some thin, rather long setae arising from the body immediately posterior to the cephalic capsule (Text-fig. 55) the distribution of which is not clear since they are either very asymmetrical in their distribution or some have been lost.

The tail is long and narrow (Text-fig. 56) with a small pre-cloacal supplement lying relatively far anterior to the cloacal opening. The spicules are stout with narrow alae and blunt, square cut distal ends (Text-fig. 58). The gubernaculum is irregular in outline with distinctly square cut lateral pieces and a fairly prominent central piece which projects between the spicules (Text-fig. 58).

DISCUSSION

This species, on the basis of the length of the cephalic setae and the number of denticles in the mandibular fields, appears to be most similar to *Oxyonchus dentatus* (Ditlevsen, 1919) but differs from it in the blunt posterior tips to the spicules, the relatively longer tail and the form of the gubernaculum—so far as it is possible to establish this latter character on the basis of the available descriptions of *O. dentatus*.

Enoplolaimus de Man, 1893

The delimitation of this genus is most uncertain and a discussion of the difficulties is given above (page 310). The following species is referred to it because several similar species have been referred to it before.

Enoplolaimus mus sp. nov.

(Text-figs. 60–73)

Material Studied. 4 ♂♂ (1 selected as holotype), 2 larvae (+ 11 ♂♂, 17 larvae in very poor condition). 32° 02′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 91). B.M. (N.H.), Reg. Nos. 1961. 281–295.

1 ♂, 1 ♀, 1 larva (all in very poor condition). 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres. WCD 90 (returned to South Africa).

1 ♀, 2 larvae (all in very poor condition). 32° 06′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 296–298.

1 ♂, 2 ♀♀ (very poor condition). 32° 05′ S./18° 16′ E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94).

Ratios			
a	*b*	*c*	*Body Length (mm.)*
31·3	4·5	16·2	4·7
35·4	4·4	15·3	4·6
33·3	4·6	15·2	5·0
34·3	4·5	15·5	4·8

Measurements (in mm. in order of body length above). Body breadth : 0·13 ; 0·15 ; 0·14 ; 0·15. Oesophagus length : 1·05 ; 1·04 ; 1·07 ; 1·09. Length of cephalic setae, anterior/long posterior/short posterior : 0·017/0·105/0·055 ; 0·018/0·103/0·058 ; 0·018/0·105/0·057 ; 0·018/0·106/0·058 ; Cephalic capsule, depth/breadth : 0·045/0·060 ; 0·048/0·062 ; 0·047/0·064 ; 0·050/0·066. Length of onchia : 0·019 ; 0·018 ; 0·019 ; 0·021. Distance of nerve ring from anterior end of body : 0·29 ; 0·30 ; 0·32 ; 0·34. Tail length : 0·30 ; 0·29 ; 0·31 ; 0·33. Cloacal diameter : 0·084 ; 0·087 ; 0·088 ; 0·091. Spicule length : 0·083 ; 0·090 ; 0·091 ; 0·094. Distance of pre-cloacal supplement anterior to cloacal opening : 0·19 ; 0·23 ; 0·25 ; 0·26.

The specimens of this species are in most cases poorly preserved which is why measurements are given for males only.

The tail in the male is long and narrow and the small pre-cloacal supplement lies relatively far anterior to the cloacal opening (Text-fig. 71). The spicules are fairly massive and squarish in outline. They expand slightly towards their posterior ends where there is a small barb-like process just proximal of the blunt ends. The blunt distal ends are split into two plate-like processes of which the more lateral is folded proximally along the length of the spicule (Text-fig. 73). The gubernaculum is slim and simple and lie close to the spicules.

DISCUSSION

Enoplolaimus mus is characterized by the short, blunt spicules with their divided distal ends, the small pre-cloacal supplement lying a relatively long way anterior to the cloacal opening, the form of the tail and the lengths of the cephalic setae.

Mesacanthion Filipjev, 1927

It should be noted that in two of the species I refer to this genus a number of cervical setae occur on the males but none are found on females or larvae.

Mesacanthion cavei sp. nov.

(Text-figs. 76–78)

MATERIAL STUDIED. 1 ♂ (holotype), 1 damaged larva (from this specimen *en face* preparation was made). 33° 58·8′ S./25° 42·2′ E. on 24.11.60 from coarse sand and broken shells at a depth of 26 metres. (SCD 212) B.M. (N.H.), Reg. No. 1963. 278.

1 ♂ (very poor condition). 32° 02′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres. WCD 91 (returned to South Africa).

Ratios

a	*b*	*c*	*Body Length (mm.)*
38·2	4·2	17·5	4·2

MEASUREMENTS (in mm.). Body breadth : 0·110. Oesophageal length : 1·00. Diameter of head : 0·060. Diameter of cephalic capsule at posterior end : 0·068. Depth of cephalic capsule : 0·052. Length of cephalic setae : 0·035 and 0·059. Length of anterior cephalic setae : 0·013. Distance of nerve ring from anterior end : 0·23. Excretory pore not seen. Tail length : 0·24. Cloacal diameter : 0·064. Length of spicules : 0·51. Length of gubernaculum : 0·038. Length of pre-cloacal supplement : 0·019. Distance of pre-cloacal supplement anterior to cloacal opening : 0·161.

The spicules are equal in length and identical in structure with simple pointed posterior ends, without alae. The gubernaculum is fairly lightly built but is slightly more complex at the proximal end than in *M. ceeus* although it clings close to the spicules along its whole length. The tail is relatively stout with, compared to *M. ceeus*, a short terminal portion (Text-fig. 78).

DISCUSSION

M. cavei is characterized by long, simple spicules and a relatively short, stout tail.

Mesacanthion ceeus sp. nov.

(Text-figs. 74–75)

MATERIAL STUDIED. 1 ♂ (Holotype), 1 larva. 33° 58′ S./25° 42·4′ E. on 24.11.60 from coarse sand and broken shells at a depth of 26 metres (SCD 212). B.M. (N.H.), Reg. Nos. 1961. 279–280.

	Ratios			
	a	*b*	*c*	*Body Length (mm.)*
Male	41·7	4·9	13·5	3·5
Larva	41·4	5·0	14·2	3·7

MEASUREMENTS (in mm. in order of body lengths). Body breadth : 0·084 ; 0·087. Oesophageal length : 0·71 ; 0·74. Diameter of head : 0·063 : 0·058. Diameter of cephalic capsule at posterior end : 0·056 ; 0·051. Depth of cephalic capsule : 0·059 ; 0·059. Length of cephalic setae : . . . .; 0·021 and 0·034. Distance of nerve ring from anterior end : 0·18 ; 0·19. Excretory pore not seen. Tail length : 0·28 ; 0·26. Cloacal or anal diameter : 0·048 ; 0·051. Length of spicules : 0·43. Length of gubernaculum : 0·031. Length of pre-cloacal supplement : 0·018. Distance of pre-cloacal supplement anterior to cloacal opening : 0·121.

The spicules are equal in length and identical in structure with distinct alae on their posterior ends which stop slightly anterior to the extreme posterior tips. The gubernaculum is very lightly built and clings very close to the spicules. The tail is relatively long and narrow, relative to *M. cavei*, and the caudal glands lie posterior to the cloacal opening (Text-fig. 75).

DISCUSSION

M. ceeus is characterized by the alate form of the spicules and the relatively long narrow tail. No cervical setae are present on the male specimen but this may not be a character of any significance since there are no cephalic setae present either which suggests that all the long setae have been lost.

Mesacanthion studiosa sp. nov.

(Text-figs. 79–90)

MATERIAL STUDIED. 2 ♂♂ (1 selected as holotype), 2 ♀♀, 2 larvae. 32° 06′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 196–201.

1 ♂. 32° 02′ S./18° 17′ E. on 2.7.61 from coarse white sand from a depth of 27 metres. WCD 91 (returned to South Africa).

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	48·4	4·3	18·7		5·5
	48·3	4·1	16·0		5·8
	53·7	4·3	16·4		5·9
Females	51·7	4·5	18·8	53·2	6·2
	52·3	4·7	20·6	55·9	6·8
Larvae	48·5	3·9	16·2		4·5
	50·0	4·1	16·0		4·8

MEASUREMENTS (in mm. in order of body lengths above). *Males.* Body breadth : 0·11 ; 0·12 ; 0·11. Oesophagus length : 1·36 ; 1·40 ; 1·38. Lengths of cephalic setae, anterior/shorter posterior/longer posterior : 0·020/0·020/0·050 ; 0·019/0·019/not present ; 0·019/0·018/0·048. Length of cervical setae : 0·030 : 0·031 ; 0·031. Cephalic capsule, depth/diameter : 0·064/0·089 ; 0·070/0·087 ; 0·062/0·091. Tail length : 0·31 ; 0·30 ; 0·36. Cloacal diameter : 0·076 ; 0·081 ; 0·075. Spicule length : 0·068 ; 0·081 ; 0·075. Distance of pre-cloacal supplement anterior to cloacal opening : 0·132 ; 0·159 ; 0·129.

Females. Body breadth : 0·12 ; 0·13. Oesophagus length : 1·37 ; 1·46. Lengths of cephalic setae, anterior/shorter posterior/longer posterior : 0·022/0·018/0·043 ; 0·020/0·018/0·048. No cervical setae. Cephalic capsule, depth/diameter : 0·975/0·107 ; 0·070/0·096. Distance of nerve ring from anterior end of body : 0·33 ; 0·31. Tail length : 0·33 ; 0·33. Anal diameter : 0·075 ; 0·075. Distance of vulva from anterior end of body : 3·3 ; 3·8.

Larvae. Body breadth : 0·093 ; 0·096. Oesophagus length : 1·16 ; 1·17. Lengths of cephalic setae, anterior/shorter posterior/longer posterior : 0·014/0·014/0·042 ; 0·014/0·014/0·046. No cervical setae. Cephalic capsule, depth/diameter : 0·054/0·076 ; 0·058/0·080. Distance of nerve ring from anterior end of body : 0·27 ; 0·28. Tail length : 0·28 ; 0·30. Anal diameter : 0·069 ; 0·074.

The tail is of about an even breadth along most of its length in both sexes (Text-fig. 88). The spicules are short with bluntly rounded distal ends, are arcuate and about the same width all along their length. There is some slight variation in outline (see Text-figs. 81 and 82). There is no gubernaculum and the pre-cloacal supplement is small and simple lying about two spicule lengths anterior to the cloacal opening.

DISCUSSION

M. studiosa is characterized by the form of the spicules, the blunt tail and the small pre-cloacal supplement.

AFRICANTHION Gen. nov.

Diagnosis on page 317

Africanthion nudus sp. nov.

(Text-figs. 91–98)

MATERIAL STUDIED. 2 ♂♂, 4 ♀♀ (+ 1 larva in poor condition). 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 93). B.M. (N.H.), Reg. Nos. 1963. 46–49 (1 ♂ returned to South Africa).

6 ♀♀, 2 larvae. 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 90). B.M. (N.H.), Reg. Nos. 1963. 50–57.

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	41·8	3·9	50·6		7·1
	46·5	3·9	43·5		7·4
Females	37·8	3·2	40·0	66·1	6·8
	42·8	3·6	42·0	65·0	8·0
	42·0	4·4	46·3	64·8	8·8
	43·6	4·2	46·0	63·0	9·2

MEASUREMENTS (in mm., in order of body lengths above). *Males.* Body breadth : 0·17 ; 0·16. Oesophagus length : 1·81 ; 1·90. Cephalic capsule, length/breadth : 0·086/0·120 ; 0·070/0·107. Lengths of cephalic setae, anterior/longer posterior/shorter posterior : 0·028/0·090/0·048 ; 0·031/0·092/0·053. Length of mandibles : 0·027 ; 0·024. Distance of nerve ring from anterior end of body : 0·31 ; 0·29. Tail length : 0·14 ; 0·17. Cloacal diameter : 0·076 ; 0·072. Spicule length : 0·089 ; 0·080. Gubernaculum length : 0·032 ; 0·028.

Females. Body breadth : 0·18 ; 0·19 ; 0·21 ; 0·21. Oesophagus length : 2·16 ; 2·21 ; 2·00 ; 2·21. Cephalic capsule, length/breadth : 0·073/0·117 ; 0·087/0·126 ; 0·086/0·121 ; 0·082/0·123. Lengths of cephalic setae, anterior/longer posterior/shorter posterior : 0·027/0·087/0·042 ; 0·031/0·099/0·054 ; 0·031/0·096/0·051 ; 0·034/0·086/0·051. Length of mandibles : 0·027 ; 0·032 ; 0·033. Distance of nerve ring from anterior end of body : 0·28 ; 0·35 ; 0·30 ; 0·31. Tail length : 0·17 ; 0·19 ; 0·19 ; 0·20. Anal diameter : 0·096 ; 0·135 ; 0·108 ; 0·111. Distance of vulva from anterior end of body : 4·5 ; 5·2 ; 5·7 ; 5·8.

The structure of the head of this species is described in detail above (page 280) and is illustrated in Text-figs. 91, 92, 93, 95 and 98. It may be noted here, however, that as a diagnostic character the posterior position of the onchia relative to the mandibular arches is highly characteristic. There are many short setae on the anterior end of the body which become progressively less common posteriorly until about the level of and posterior to the nerve ring they are very rare.

The male tail is very characteristic. It is short and stout (Text-fig. 94) without a pre-cloacal supplementary organ of any kind. There is, however, a series of six stout short setae on the mid-ventral line of the body, about two spicule lengths anterior to the cloacal opening, which appear to replace the supplement found in this region in all other Enoplidae. There are, in addition, two files of more normal thin setae, ventro-lateral in position, running between the cloacal opening and the stout ventral setae (Text-figs. 94 and 96). The spicules are short, massive and curved at the distal ends where they finish in a sharp hook-like point (Text-fig. 97). The gubernaculum is small with a complex distal end and lies close to the spicules.

DISCUSSION

This species is apparently similar to those generally referred to the genus *Mesacanthion* but differs in the structure of the mandibles, the form of the male reproductive apparatus with the blunt spicules and elaborate, small gubernaculum and differs from all other Enoplidae in the presence of stout setae on the ventral surface of the male anterior to the cloacal opening in the area in which the pre-cloacal supplement is usually found. I, therefore, refer it to a new genus, *Africanthion*, which may be diagnosed thus :

> Enoplidae : mandibles with lateral processes very well developed and mandibular walls fairly narrow in optical section ; mandibular plate thin ; onchia slightly unequal, dorsal smaller than ventro-lateral ; onchia lying far posterior to mandibles ; cephalic setae arising from middle of cephalic capsule.
>
> MALES : spicules short and stout ; gubernaculum small and complex ; pre-cloacal supplement replaced by a file of stout, short setae.
>
> TYPE SPECIES : *Africanthion nudus* sp. nov.

Trileptium Cobb, 1933

It is with some reservations that I refer the species described below to this genus but it appears to correspond to the descriptions which have been given by other authors sufficiently closely to warrant this allocation.

Trileptium ayum sp. nov.

(Text-figs. 99–102)

MATERIAL STUDIED. 1 ♂ (Holotype), 1 ♀, 1 ♀ 4th-stage larva, 1 larva. 33° 58·8′ S./25° 42·2′ E. on 24.11.60 from coarse sand and broken shells at a depth of 26 metres (SCD 212). B.M. (N.H.), Reg. Nos. 1963. 139–141.

1 ♀. 32° 02′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 91) (Very poor condition).

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Male	50·8	4·9	31·0		6·6
Female	48·8	4·6	28·2	63·9	8·3
Larva (♀)	47·5	4·6	32·8	49·1	5·7
Larva	41·7	3·4	24·0		3·5

MEASUREMENTS (in mm.). *Male* ; *female*. Body breadth : 0·13 ; 0·17. Oesophageal length : 1·34 ; 1·79. Diameter of head : 0·034 ; 0·045. Diameter of cephalic capsule at posterior edge : 0·042 ; 0·062. Depth of cephalic capsule : 0·036 ; 0·047. Length of cephalic setae : 0·024 and 0·081 ; 0·028 and 0·099. Distance of nerve ring from anterior end : 0·25 ; 0·20. Excretory pore not seen. Tail length : 0·213 ; 0·294. Cloacal or anal diameter : 0·075 ; 0·120. Length of spicules : 0·65. Length of gubernaculum : 0·058. Length of pre-cloacal supplement : 0·013. Distance of pre-cloacal supplement anterior to cloacal opening : 0·046. Distance of vulva from anterior end : 5·3. Cervical setae and long body setae were seen only in the male where they were 0·027 to 0·060 mm. and 0·049–0·054 mm. in length respectively.

Larvae (4th-stage ♀ first). Body breadth : 0·12 ; 0·084. Oesophageal length : 1·24 ; 1·03. Diameter of head : 0·039 ; 0·030. Diameter of cephalic capsule at posterior edge : 0·047 ; 0·025. Depth of cephalic capsule : 0·039 ; 0·029. Length of cephalic setae : 0·030 and 0·081 ; . . . and 0·037. Distance of nerve ring from anterior end : 0·024 ; 0·020. Excretory pore not seen. Tail length : 0·174 ; 0·146. Anal diameter : 0·072 ; 0·057. Distance of vulva from anterior end : 2·8.

The inner pouch of the cephalic slit is very prominent (Text-figs. 99 and 100) and the cephalic setae are very long. The amphids are small, lying just posterior to the posterior edge of the cephalic capsule, and slightly ventral in position. The mouth is closed by three small lip-flaps, the three onchia are small and lie far forward between the mandibles (Text-fig. 101), the cephalic capsule is poorly developed and there are several long cervical setae present on the male only. The tail is short and stout in both sexes (Text-fig. 102).

The spicules are long and thin, equal in length and without alae. The gubernaculum is small and clings close to the spicules while the simple pre-cloacal supplement lies relatively close to the cloacal opening (Text-fig. 102). There are two opposed testes.

The female reproductive system is double with reflexed, opposed ovaries. The eggs are large, 0·40 × 0·11 mm. in size.

DISCUSSION

The genus *Trileptium* currently contains four species, *T. subterraneum* (Gerlach, 1952), *T. salvadoriense* Gerlach, 1955, *T. gullata* (Cobb, 1920), *T. iacobinum* Wieser, 1959, from which the present species can be distinquished by the following combination of characters : pre-cloacal supplement present, gubernaculum without an apophosis, all three onchia present although rather small.

Thoracostomopsis Ditlevsen, 1919

Filipjev (1927) proposes a new subfamily for this genus because both he and Ditlevsen (1919) misunderstood the structure of the head and thought it contained a spear. Four species have been previously referred to the genus, *T. barbata* Ditlevsen, 1919 (type species) ; *T. ditlevseni*, *T. galeata* and *T. longissima* all three described and named by Filipjev (1927). Two of these species, *T. barbata* and

T. galeata, are only known on the basis of females. In view of the great similarities between the species I describe below and *T. barbata*, in the structure of the head, and the markedly different type of head described by Filipjev for his species it is possible that more than one genus should be recognized. The genus, although well founded and very distinct from any other, can only be treated as one of the several types of modification of the Enoplidae and certainly does not, at present, warrant separation in a distinct subfamily.

Thoracostomopsis carolae sp. nov.

(Text-figs. 103–109)

Material Studied. 1 ♂ (Holotype), 2 ♀♀. 32° 05′ S./18° 16′ E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. Nos. 1963. 180–182.

1 ♀. 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 93). B.M. (N.H.), Reg. No. 1963. 183.

1 ♂ (+ 1 ♂, 1 ♀ in poor condition). 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres. WCD 90 (returned to South Africa).

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Males (holotype)	75·5	10·0	39·4		8·3
	67·4	9·3	31·2		8·1
Females	60·0	9·7	35·5	55·1	7·8
	63·1	10·0	39·4	54·7	9·5
	68·5	10·3	41·6	55·2	9·6

Measurements (in mm. in order of body lengths above). *Males.* Body breadth: 0·11 ; 0·12. Oesophagus length : 0·83 ; 0·87. Mandible length : 0·012 ; 0·013. Cephalic capsule, length/diameter : 0·029/0·031 ; 0·031/0·033. Length setae, anterior/longer posterior/shorter posterior : 0·014/0·068/0·030 ; 0·013/0·065/0·032. Length of cervical setae on holotype : 0·032 ; 0·046. Tail length : 0·21 ; 0·26. Cloacal diameter : 0·071 ; 0·083. Spicule length : 0·165 ; 0·176. Gubernaculum length : 0·045 ; 0·067. Distance of pre-cloacal supplement anterior to cloacal opening : 0·141 ; 0·154.

Females. Body breadth : 0·13 ; 0·15 ; 0·14. Oesophagus length : 0·80 ; 0·85 ; 0·95. Mandible length : 0·014 ; 0·011 ; 0·012. Cephalic capsule, length/breadth : 0·028/0·033 ; 0·030/0·034 ; 0·032/0·035. Length of setae, anterior/longer/longer posterior/shorter posterior : 0·012/0·058/0·031 ; 0·014/0·063/0·029 ; 0·014/0·066/0·028. Tail length : 0·22 ; 0·22 ; 0·23. Anal diameter : 0·069 ; 0·067 ; 0·066. Distance of vulva from anterior end : 4·3 ; 5·2 ; 5·3.

The most spectacular morphological feature of this animal is the highly modified head and oesophagus which are described above in detail (page 281) and illustrated in Text-figs. 103–107. The anterior end of the body shows a slight sexual dimorphism in that there are several long setae just posterior to the cephalic capsule in the male which do not occur in the female. The tail is fairly short and stout in both sexes (Text-fig. 108). In the male the spicules are simple and needle-like with sharp distal ends and without alae. The gubernaculum is small and lies close to the spicules. There is a simple pre-cloacal supplement and a series of long stoutish ventro-lateral setae running on both sides of the body between the cloacal opening and the supplement.

DISCUSSION

The present species differs from the previously described males in the possession of long, thin spicules—they are relatively short and stout in the two known species. It also differs from *T. galeata* and *T. longissima* in the amphids not lying posterior to the cephalic capsule. Filipjev (1927) in his treatment of this genus refers to the amphids of *T. barbata* as lying " Au milieu de la capsule céph. " but this is an error since Ditlevsen specifically says " Lateral organs (= amphids) are not seen in my specimen ". Ditlevsen does, however, refer to " In the very front-end of the body the spear is supported by short chitenous rods . . . " which are probably the mandibles. *T. barbata* was described from one " scarcely mature female . . . " and its status must be considered uncertain. The present species appears to differ from it in having relatively shorter cephalic setae.

Enoplus Dujardin, 1845

This genus, the type of the family, is one of the most easily recognized among the marine members of the Order. The reduction and concentration of the mandibular and onchial complexes to form one massive median organ in each lip is so spectacular that there is no difficulty in identifying its members. Two species are present in the collections, one of which is new and the other previously described.

Enoplus harlockae sp. nov.

(Text-figs. 110, 113, 115)

MATERIAL STUDIED. 1 ♂ (holotype), 1 ♀, 1 larva. 32° 06′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 130–132.

Ratios

	a	*b*	*c*	*V*	*Body Length (mm.)*
Male	28·0	5·5	16·8		4·2
Female	25·6	5·6	14·1	56·1	4·1
Larva	23·3	4·7	13·3		2·8

MEASUREMENTS (in mm.). *Male.* Body breadth : 0·15. Oesophagus length : 0·76. Length of cephalic setae, long/short : 0·020/0·018. Diameter of cephalic capsule at posterior edge : 0·066. Distance of eye spots from anterior end of body: 0·069. Length of mandibles : 0·026. Distance of nerve ring from anterior end of body : 0·32. Distance of excretory pore from anterior end of body : 0·25. Tail length : 0·25. Cloacal diameter : 0·12. Spicule length : 0·144. Gubernaculum length : 0·069. Pre-cloacal supplement, length/distance anterior to cloacal opening : 0·099/0·24.

Female. Body breadth : 0·16. Oesophagus length : 0·73. Length of cephalic setae, long/short : 0·018/0·013. Diameter of cephalic capsule at posterior edge : 0·069. Distance of eye spots from anterior end of body : 0·069. Length of mandibles : 0·026. Distance of nerve ring from anterior end of body : 0·33. Distance of excretory pore from anterior end of body : 0·26. Tail length : 0·29. Anal diameter : 0·11. Distance of vulva from anterior end of body : 2·3. Size of egg : 0·096 × 0·126.

Larva. Body breadth : 0·12. Oesophagus length : 0·60. Length of cephalic setae, long/short : 0·018/0·015. Diameter of cephalic capsule at posterior edge : 0·051. Distance of eye spots from anterior end of body : 0·051. Length of mandibles : 0·021. Distance of nerve ring from anterior end of body : 0·27. Distance of excretory pore from anterior end of body : 0·22. Tail length : 0·21. Anal diameter : 0·084.

The amphids lie on the posterior edge of the cephalic capsule (Text-fig. 111) and the head is otherwise typical (see page 282). The tail is fairly short and stout with a short, narrow terminal part (Text-fig. 115) in both sexes.

In the male the spicules are stout and S-shaped with two large barb-like plates and apparently very narrow alae (Text-fig. 113). The gubernaculum is short and the median and the lateral pieces curve upwards to enfold the spicules (Text-fig. 113). The pre-cloacal supplement is straight and swollen at its proximal end and the distal end is divided into three hook-like processes (this appears to be common in the supplement of *Enoplus* species although it seems to have been mentioned only by Mawson (1958) in *E. michaelseni*). There are the usual long, stout setae on the ventro-lateral surfaces of the body between the cloacal opening and the pre-cloacal supplement (Text-fig. 115).

DISCUSSION

This species is most similar in general appearance to *E. meridionalis* Steiner, 1922 but is characterized by the form of the pre-cloacal supplement, the short, S-shaped spicules with only two plates and the shape of the gubernaculum, which appears to be unique. The position of this latter structure is unlikely to be due to muscle contraction because of the relationships between the side pieces and the median joining piece.

Enoplus michaelseni Linstow, 1896

MATERIAL STUDIED. 1 ♂, 1 larvae. 32° 06′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. No. 1963. 137–138.

Ratios

a	*b*	*c*	*Body Length (male) (mm.)*
44·4	8·3	27·3	6·0

MEASUREMENTS (in mm.). *Male.* Body breadth: 0·14. Oesophagus length: 0·72. Length of cephalic setae, long/short : 0·023/0·015. Diameter of cephalic capsule at posterior end : 0·075. Distance of eye spots from anterior end of body : 0·081.

Distance of nerve ring from anterior end of body : 0·33. Distance of excretory pore from anterior end of body : 0·25. Length of mandibles : 0·033. Tail length : 0·22. Cloacal diameter : 0·096. Spicule length : 0·144. Gubernaculum length : 0·075. Pre-cloacal supplement, length/distance anterior to cloacal opening : 0·075/0·19.

This species is typical of the genus and is characterized by the amphids lying anterior to the posterior edge of the cephalic capsule (Text-fig. 112), the large trumpet-shaped pre-cloacal supplement and the form of the spicules and gubernaculum (Text-fig. 114). De Man's (1904) figures of this species are particularly good and I differ from him only in finding a ventral spine on the distal ends of the gubernaculum. The spicules bear five large plates close together and a small more distal one.

Rhabdodemania Baylis and Daubney, 1926

As Filipjev (1934) points out this is a very distinctive genus for which he creates a new subfamily. However, as Wieser (1959) suggests, the buccal cavity may be interpreted as composed of three modified mandibles (see above, page 282) but this does not simplify the relationships of the genus which is still very different from the typical Enoplidae facies. The onchial cavity has expanded until it dominates the anterior end of the body, the cephalic capsule appears to be lost and the buccal cavity is reduced to a shallow space. The genus is probably near the Enchilidiinae/Eurystomatinae group but, provisionally, I shall refer it to the family Enoplidae.

Rhabdodemania nancyae sp. nov.

(Text-figs. 116–120)

MATERIAL STUDIED. 10 + ♂♂, 10 + ♀♀. 35° 58·8′ S./25° 42·2′ E. on 24.11.60 from coarse sand and broken shells at a depth of 26 metres (SCD 212). B.M. (N.H.), Reg. Nos 1963. 299–318.

3 ♂♂, 5 ♀♀, 4 larva. 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres. WCD 93 (returned to South Africa).

6 ♂♂, 8 ♀♀, 3 larvae. 35° 05′ S./18° 16′ E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. Nos. 1963. 319–335.

Ratios

	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	51·3	6·8	20·6		3·7
	46·9	6·9	22·4		3·8
	48·1	7·1	21·7		3·9
Females	48·7	7·0	23·1	59·5	3·7
	49·4	7·2	21·1	60·5	3·8
	45·9	7·0	20·5	56·4	3·9

MEASUREMENTS (in mm., in order of body lengths above). *Males.* Body breadth : 0·072 ; 0·081 ; 0·081. Oesophagus length : 0·54 ; 0·55 ; 0·55. Diameter of head : 0·014 ; 0·014 ; 0·016. Depth of buccal cavity : 0·017 ;

0·016 ; 0·018. Width of buccal cavity : 0·008 ; 0·009 ; 0·011. Length of cephalic setae, long/short : 0·011/0·006 ; 0·012/0·007 ; 0·012/0·007. Distance of nerve ring from anterior end of body : 0·21 ; 0·25 ; 0·26. Distance of excretory pore from anterior end of body : 0·022 ; 0·024 ; 0·025. Tail length : 0·18 ; 0·17 ; 0·18. Cloacal diameter : 0·058 ; 0·058 ; 0·058. Length of spicules : 0·051 ; 0·058 ; 0·053. Length of gubernaculum : 0·029 ; 0·032 ; 0·035.

Females. Body breadth : 0·076 ; 0·071 ; 0·085. Oesophagus length : 0·53 ; 0·53 ; 0·56. Diameter of head : 0·013 ; 0·013 ; 0·015. Depth of buccal cavity : 0·018 ; 0·017 ; 0·019. Width of buccal cavity : 0·008 ; 0·010 ; 0·011. Distance of nerve ring from anterior end of body : 0·23 ; 0·24 ; 0·26. Distance of excretory pore from anterior end of body : 0·020 ; 0·023 ; 0·024. Tail length : 0·16 ; 0·18 ; 0·19. Anal diameter : 0·054 ; 0·057 ; 0·058. Distance of vulva from anterior end of body : 2·2 ; 2·3 ; 2·2.

The mouth opening appears to be large and circular but it is very difficult to be sure because of the size and condition of the specimens but the lining of the mouth opening is striated (Text-figs. 117 and 121). Wieser (1959) refers to " . . . strongly developed, cushion-like " lips but he is clearly only referring to the stout projecting anterior end of the body. A very poorly developed cephalic capsule appears to be present but this, also, is uncertain. The oesophagus expands evenly along its length and is cellular posteriorly. There is a large dorsal onchium and two small, equal ventro-lateral onchia. The tail is stout and blunt posteriorly and the three caudal glands lie posterior to the cloacal opening (Text-fig. 120).

The spicules are of the form typical for the genus, equal in length and identical in structure with rather square distal ends. The gubernaculum is slim and lightly built and there is no pre-cloacal supplement (Text-fig. 119). There is only one testis.

The reproductive system is double with opposed uteri and reflexed ovaries. The oviducts are modified as spermathecae and the eggs are relatively very large, 0.189 mm. × 0.045 mm. and 0·200 mm. × 0·048 mm. for example.

DISCUSSION

The species described above is clearly distinct from the five species currently referred to the genus. It differs from *R. major* (Southern, 1914), *R. coronata* Gerlach, 1952 and *R. illgi* Wieser, 1959 in having the cephalic setae arranged in one circle and not two. It appears to differ from the two remaining species, *R. minor* (Southern, 1914) and *R. gracilis* (Ditlevsen, 1919), in the form of the spicules but I am not sure how reliable this character is although Filipjev (1927) stresses it in considering *R. minor* and *R. gracilis*. *R. nancyae* is, however, easily distinguished from all the previous species by the small size of the ventro-lateral onchia which, compared with the dorsal onchium, are almost wholly reduced.

R. nancyae is characterized by cephalic setae in one circle, square-ended spicules and greatly reduced ventro-lateral onchia.

Family **LEPTOSOMATIDAE** Filipjev, 1916

This family is quite distinct from the Enoplidae and Phanodermatidae in the structure of the head and the form of the oesophagus. There are, however, two distinct groups within it as at present constituted. As Mawson (1956) rightly points out, keys to the Leptosomatidae tend to divorce *Thoracostoma* from *Leptosomatum* to which it shows clear affinities. *Leptosomatum* Bastian, 1865, *Leptosomatides* Filipjev, 1918, *Paraleptosomatides* Mawson, 1956, *Corythostoma* Wieser, 1956, *Synonchoides* Wieser, 1956 and *Thoracostoma* Marion, 1870 clearly form a distinctive group on the form of the tail, the spicules, and also the structure of the head. Wieser (1956) proposes *Corythosoma* and *Synonoides* as subgenera of *Thoracostoma* but there is more reason to consider them distinct genera than there is for treating *Paraleptosomatides*, for example, as a distinct genus. The genera *Macronchus* gen. nov., *Jagerskioldia* Filipjev, 1916, *Synonchus* Cobb, 1894, *Cylicolaimus* de Man 1889a and *Platycoma* Cobb, 1893 form another group with which *Barbonema* Filipjev, 1927 and *Parabarbonema* gen. nov. should probably be associated. Possibly *Platycomopsis* Ditlevsen, 1926 and *Metacylicolaimus* Schuurmans Stekhoven, 1946 also belong with this group. The genera *Anticoma* Bastian, 1865, and *Paranticoma* Micoletzky, 1930 are the only forms in the family in which the pre-cloacal supplement is rod-like but this I interpret as a primitive character and would not consider it any reason to transfer these two genera from the family. The most that can safely be said about this family is that there are two different groups of highly evolved genera, the first and second adumbrated above, but as the information on so many of the others is insufficient the family is best left as one major undivided group. It may be diagnosed as follows :

> Enoplida : posterior part of oesophagus never showing " cellular " appearance ; amphids pocket-like ; buccal cavity never large ; onchia carried far forward and supplied by muscles passing through cephalic vesicle ; pre-cloacal supplements generally papilloid, if not, then simple rod-like ; spicules never very complex with plates ; cephalic capsule in highly evolved forms very prominent ; cephalic ring not prominent.
>
> TYPE GENUS : *Leptosomatum* Bastian, 1865.

Anticoma Bastian, 1865

This genus is usually defined as lacking a cephalic capsule and onchia but in fact several species with both these features have previously been referred to the genus. The species I describe below is so equipped but I prefer to refer it to *Anticoma* rather than attempt to untangle the genus as at present constituted.

Anticoma chitwoodi sp. nov.

(Text-figs. 122–131)

MATERIAL STUDIED. 2 ♂♂ (1 selected as holotype), 1 ♀. 34° 02′S./23° 48·4′ E. on 29.11.60 from sand, mud and rock at a depth of 50 metres (SCD 220). B.M. (N.H.), Reg. Nos. 1963. 42–44.

Ratios

	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	48·8	5·9	7·5		4·0
	51·8	5·5	7·7		4·3
Female	47·4	6·4	7·9	43·5	4·6

MEASUREMENTS (in mm., in order of body lengths above). *Males.* Body breadth : 0·082 ; 0·083. Oesophagus length : 0·68 ; 0·78. Cephalic capsule, depth/diameter at posterior edge : 0·013/0·021 ; 0·012/0·018. Length of cephalic setae, long/short : 0·018/0·011 ; 0·017/0·011. Distance of cervical setae from anterior end of body : 0·054 ; 0·047. Distance of nerve ring from anterior end of body : 0·29 ; 0·32. Distance of excretory pore from anterior end of body : 0·19 ; 0·23. Tail length : 0·53 ; 0·56. Cloacal diameter : 0·053 ; 0·069. Spicule length : 0·084 ; 0·099. Gubernaculum length : 0·032 ; 0·036. Length of pre-cloacal supplement : 0·017 ; 0·015. Distance of pre-cloacal supplement anterior to cloacal opening : 0·078 ; 0·072.

Female. Body breadth : 0·097. Oesophagus length : 0·72. Cephalic capsule, depth/diameter at posterior edge : 0·011/0·024. Length of cephalic setae, long/short : 0·018/0·012. Distance of cervical setae from anterior end of body : 0·056. Distance of nerve ring from anterior end of body : 0·31. Distance of excretory pore from anterior end of body : 0·22. Tail length : 0·58. Anal diameter : 0·052. Distance of vulva from anterior end of body : 2·0. The eggs are 0·189 mm. × 0.073 mm.

The head is rounded in outline with a distinct cephalic capsule on the posterior edge of which lie the openings of the amphids (Text-fig. 126). The capsule in one male specimen is fenestrate, as is shown in Text-figs. 126–131. The anterior end of each sector of the oesophagus carries a small onchium which arises from a thickening of the cuticular covering of the oesophagus (Text-figs. 122 and 125). The cervical setae vary from three to five in number.

The tail in both sexes narrows rapidly to end in a very long terminal filament (Text-fig. 124). In the male the spicules are lightly built with wide alae and the gubernaculum is fairly long with prominent lateral pieces which are blunt posteriorly (Text-fig. 123). The pre-cloacal supplement is rod-like and two rows of stout setae are carried on the ventro-lateral aspects of the body between the supplement and the cloacal opening (Text-fig. 124).

DISCUSSION

The cephalic capsule appears to be more strongly developed than is usually the case but I am not sure that this is a good character as it was best seen in uncleared specimens. However, even in those cleared with glycerine, its presence could easily be established. The species is distinct from all others in the form of the lightly built spicules, the structure of the gubernaculum, the great length of the tail, the presence of distinct onchia at the anterior end of the oesophagus and the position of the excretory pore. *A. chitwoodi* appears to be most similar to *A. columba* Wieser, 1953—which is also reported from a subantarctic locality, MacRobertson Land by Mawson (1958a)—but differs in the extreme length of the tail, the more anterior position of the amphid, the less prominent pre-cloacal supplement (probably an unreliable character), the structure of the spicules and gubernaculum. It is also similar to *A. kerguelenensis* Mawson, 1958a from which it differs in the more massive gubernaculum, the form of the spicules and the prominent amphids which lie relatively farther anterior in position.

PARABARBONEMA gen. nov.

The species I describe below was at first considered to belong to the genus *Barbonema* Filipjev, 1927 but it is clear that a new genus is required for its reception. Filipjev (1927) describes the spicules in *B. setifera* Filipjev, 1927 as apparently incompletely developed while Gerlach (1956) in describing his new species, *B. horridum*, is unable to decide whether there are two or only one spicule present and later, in describing *B. flagrum* Gerlach, 1957, makes the same comment. The spicules and gubernaculum in the species described below are very similar to those described by Filipjev and Gerlach but these authors are agreed that there is no pre-cloacal supplement in any of their species and the tail is long with a semi-flagellate end. In all three the amphids lie posterior to the longest post-cephalic setae (although in the case of *B. flagrum* this is a little uncertain) while in the present species they lie anterior to them and in all three the labial sense organs are (?) setose while in this species they are not. In view of this combination of a short tail, a pre-cloacal supplement, the position of the amphids on the posterior edge of the cephalic capsule and the form of the labial sense organs I propose to refer this species to a new genus, *Parabarbonema*. It may be pointed out here that *B. flagrum* appears to be very different from the other two species referred to *Barbonema* and will probably warrant separation in a distinct genus when more species are known. The new genus *Parabarbonema* may be diagnosed thus :

> Leptosomatidae : cephalic capsule well developed, unlobed ; labial sense organs papillate; anterior ends of oesophageal sectors modified as broad onchia; amphids prominent, opening on posterior edge of cephalic capsule ; all long cervical setae posterior to amphids ; tail short and stout in both sexes.
>
> MALE : papillate pre-cloacal supplement present ; spicules short and stout ; gubernaculum large, indistinct, with large thin sheets of cuticle enfolding spicules.
>
> TYPE SPECIES : *Parabarbonema barba* sp. nov.

Parabarbonema barba sp. nov.

(Text-figs. 32–137)

MATERIAL STUDIED. 12 ♂♂ (1 selected as holotype), 17 ♀♀, 29 larvae. 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 90). B.M. (N.H.), Reg. Nos. 1963. 202–259.

2 ♂♂ (+ 1 ♂ in very poor condition). 32° 05′ S./18° 16′ E. on 2.7.61 from khaki mud at a depth of 54 metres. WCD 94 (returned to South Africa).

6 ♂♂, 3 ♀♀, 3 larvae. 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand from a depth of 39 metres (WCD 93). B.M. (N.H.), Reg. Nos. 1963. 260–271.

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	96·0	6·3	53·3		9·6
	98·0	7·1	57·6		9·8
	108·9	7·5	70·0		9·8
	97·3	8·4	62·9		10·7
Females	93·0	6·3	42·3	71·0	9·3
	99·1	7·6	49·5	63·6	10·9
Larva	91·7	7·8	53·1		10·1

MEASUREMENTS (in mm. in order of body lengths above). *Males.* Body breadth : 0·10 ; 0·099 ; 0·091 ; 0·11. Oesophagus length : 1·52 ; 1·37 ; 1·30 ; 1·28. Diameter of head : 0·027 ; 0·029 ; 0·025 ; 0·024. Diameter of cephalic capsule at posterior end : 0·030 ; 0·031 ; 0·029 ; 0·028. Distance of amphid from anterior end of body (= depth of cephalic capsule) : 0·019 ; 0·021 ; 0·017 ; 0·016. Length of cephalic setae : 0·029 ; 0·029 ; 0·024 ; 0·024. Length of cervical setae, long pair immediately posterior to amphid/shorter setae scattered posterior to paired setae : 0·029/0·022 ; 0·028/0·023 ; 0·023/0·020 ; 0·024/0·022. Distance of nerve ring from anterior end of body : 0·41 ; 0·47 ; 0·43 ; 0·43. Distance of excretory pore from the anterior end could be measured only in the 10·7 mm. long specimen where it is 0·12. Tail length : 0·18 ; 0·17 ; 0·14 ; 0·17. Cloacal diameter : 0·08 ; 0·08 ; 0·08 ; 0·09. Spicule length : 0·082 ; 0·079 ; 0·063 ; 0·084. Distance of pre-cloacal supplement anterior to cloacal opening : 0·12 ; 0·098 ; 0·090 ; 0·11.

Females. Body breadth : 0·099 ; 0·11. Oesophagus length : 1·48 ; 1·43. Diameter of head : 0·020 ; 0·028. Diameter of cephalic capsule at posterior end : 0·036 ; 0·034. Distance of amphid from anterior end of body (= depth of cephalic capsule) : 0·022 ; 0·020. Length of cephalic setae : 0·027 ; 0·029. Length of cervical setae, long pair immediately posterior to amphid/shorter setae scattered posterior to paired setae : 0·026/0·026 ; 0·028/0·026. Distance of nerve ring from anterior end of body : 0·043 ; 0·046. Excretory pore not seen. Tail length : 0·22 ; 0·22. Anal diameter : 0·09 ; 0·08. Distance of vulva from anterior end of body : 6·6 ; 7·0.

Larva. Body breadth : 0·11. Oesophagus length : 1·37. Diameter of head : 0·028. Diameter of cephalic capsule at posterior end : 0·020. Distance of amphid from anterior end of body (= depth of cephalic capsule) : 0·019. Length of cephalic setae : 0·028. Length of cervical setae, long pair immediately posterior to amphid/shorter setae scattered posterior to paired setae : 0·027/0·023. Distance of nerve ring from anterior end of body : 0·39. Excretory pore not seen. Tail length : 0·19. Anal diameter : 0·08.

The head bears the usual ten long setae and an inner circle of six papillae. The long setae are about the same length and I have been unable to distinguish between sets of long and short (Text-figs. 132 and 133). The cephalic capsule is simple but distinct and the openings of the large pocket amphids lie on the posterior edge of the capsule (Text-fig. 133). Immediately posterior to the amphids lie two long, equal setae which arise very close together. These setae are long, about the same length as the cephalic setae (see measurements above), and are followed by a series of shorter setae on the anterior part of the body. These body setae occur in eight files over roughly the anterior seventh of the length of the oesophagus becoming smaller and further apart posteriorly. The oesophagus is non-muscular, without any posterior swelling but with a well developed oesophageal-intestinal valve.

The tail is short and stout in both sexes and ends in a blunt, rounded tip (Text-fig. 134). In the male there is a papillate pre-cloacal supplement similar to that occurring in the genus *Thoracostoma*. A series of ventro-lateral, stout setae occur on the tail and on the body between the cloacal opening and the supplement. The spicules are equal and identical and are bluntly rounded posteriorly. The gubernaculum is in two parts and is developed as an extensive, thin sheet round both spicules. This sheet arises from well developed lateral portions—lying dorsal to the spicules—which are modified distally as relatively massive, apparently slightly toothed, regions which are rather similar in appearance to the distal ends of the gubernaculum in species of *Cyatholaimus* (Text-figs. 135 and 136).

MACRONCHUS gen. nov.

One species which is present in the collection in very large numbers is most similar to those referred to the genus *Synonchus* in particular and the genera *Jagerskioldia* and *Cylicolaimus* in general but differs from them in possessing two pre-cloacal supplements, very massive spicules, a massive dentate distal end to the gubernaculum and large onchia developed from the centre of each sector of the oesophagus. It is very distinctive and I propose to refer it to a new genus, *Macronchus*.

Leptosomatidae : cephalic capsule narrow ; large median onchia on each sector of oesophagus ; small wholly cuticular odontia developed from lining of buccal cavity.

Male : two pre-cloacal supplements, more anterior large and double, more posterior single and papillate ; body swollen anterior to cloacal opening, bearing long stout setae in several rows ventro-laterally ; gubernaculum with massive dentate distal ends.

Type species : *Macronchus shealsi* sp. nov.

Macronchus shealsi sp. nov.
(Text-figs. 138–147)

Material Studied. 13 ♂♂ (1 selected as holotype), 11 ♀♀, 9 larvae. 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 90). B.M. (N.H.), Reg. Nos. 1963. 59–91.

11 ♂♂, 12 ♀♀, 8 larvae. 32° 05′ S./18° 16′ E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. Nos. 1963. 93–123.

5 ♂♂. 32° 05′ S./18° 16′ E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 102). B.M. (N.H.), Reg. Nos. 1963. 124–128.

1 larva. 32° 02′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 91). B.M. (N.H.) Reg. No. 1963. 92.

15 ♂♂, 18 ♀♀, 22 larvae. 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres. WCD 93 (returned to South Africa).

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	50·0	6·4	25·0		11·0
	53·2	6·8	25·4		11·7
	56·7	7·1	29·0		11·9
	55·9	6·9	25·6		12·3
Females	57·1	7·1	27·9	46·5	12·0
	56·8	7·6	27·2	48·9	12·5
	60·0	7·0	26·4	53·8	13·2
Larvae (4th stage ♀)	52·4	7·0	25·6	49·1	11·0
	53·0	7·5	26·5	49·2	12·2

MEASUREMENTS (in mm., in order of body lengths above). *Males.* Body breadth : 0·22 ; 0·22 ; 0·21 ; 0·22. Oesophagus length : 1·72 ; 1·71 ; 1·68 ; 1·77. Diameter of head : 0·054 ; 0·049 ; 0·041 ; 0·057. Length of cephalic setae, long/short : 0·014/0·013 ; 0·014/0·013 ; 0·014/0·012 ; 0·015/0·013. Distance of nerve ring from anterior end of body : 0·49 ; 0·49 ; 0·46 ; 0·51. Tail length : 0·44 ; 0·41 ; 0·41 ; 0·48. Cloacal diameter : 0·192 ; 0·176 ; 0·168 ; 0·188 Spicule length : 0·216 ; 0·214 ; 0·192 ; 0·219. Gubernaculum length : 0·099 ; 0·098 ; 0·096 ; 0·102. Distance of first pre-cloacal supplement anterior to cloacal opening : 0·210 ; 0·206 ; 0·195 ; 0·214. Distance of second (i.e. more anterior) pre-cloacal supplement anterior to cloacal opening : 0·47 ; 0·47 ; 0·44 ; 0·47.

Females. Body breadth : 0·21 ; 0·22 ; 0·22. Oesophagus length : 1·69 ; 1·64 ; 1·86. Diameter of head : 0·054 ; 0·052 ; 0·059. Length of cephalic setae, long/short : 0·014/0·013 ; 0·013/0·012 ; 0·013/0·012. Distance of nerve ring from anterior end of body : 0·47 ; 0·47 ; 0·48. Tail length : 0·43 ; 0·46 ; 0·50. Anal diameter : 0·12 ; 0·13 ; 0·14. Distance of vulva from anterior end of body : 5·6 ; 6·1 ; 6·9.

Larvae. Body breadth : 0·21 ; 0·23. Oesophagus length : 1·56 ; 1·62. Diameter of head : 0·061 ; 0·066. Length of cephalic setae, long/short : 0·014/0·012 ; 0·014/0·013. Distance of nerve ring from anterior end of body : 0·47 ; 0·52. Tail length : 0·43 ; 0·46. Anal diameter : 0·14 ; 0·13. Distance of vulva from anterior end of body : 5·4 ; 6·0.

The head is bluntly rounded with a narrow cephalic capsule. There is an inner circle of six sessile papillae and an outer circle of ten setae of which six are longer than the remaining four (Text-fig. 143). The median onchium on each lip is large, prominent and the same size on all three lips. The small amphids lie posterior to the cephalic capsule. There is a series of setae on the anterior part of the body posterior to the head (Text-fig. 142) arranged in distinct groups. A series of wholly cuticular teeth arise from the cuticular lining of the buccal cavity (Text-figs. 138, 139 and 141). The head is relatively large, i.e. the body does not narrow markedly anteriorly. The oesophagus is not muscular posteriorly. The ventro-lateral oesophageal glands open at the bases of the large onchia while the dorsal gland duct opens through a small denticle-like structure some distance posterior to the large median onchium (Text-fig. 141).

The tail is stout in both sexes with a narrow terminal zone (Text-fig. 145). In the male there is a definite ventral bump immediately anterior to the beginning of this narrow zone which is due to a thickening of the cuticle. The male tail is further characterized by the presence of two pre-cloacal supplementary structures (Text-figs. 145 and 147). Of these the more anterior is the larger and consists of a raised area of cuticle, supplied by special musculature, in which are two slightly curved rows of small rods pierced by channels (Text-fig. 144). The more posterior supplement is more papillate in appearance but when studied from the ventral aspect is supported by a thickening of the cuticle as shown in Text-fig. 147. The body immediately anterior to the cloacal opening is markedly wider than at any other point on the body (see Text-fig. 147) and this area is covered on each ventro-lateral area by a series of long, stout setae. The most lateral setae are the longest and stoutest and become increasingly smaller and slimmer towards the ventral surface. The spicules are equal, identical and massive (Text-figs. 146 and 147) with narrow alae. Note that the outer part of the spicule along the non-alate side is much thicker than along the alate surface. The gubernaculum is relatively small in two parts with distinctly toothed, relatively massive distal heads (Text-figs. 146 and 147).

Thoracostoma Marion, 1870

This genus is with *Enoplus* one of the most easily recognized in any sample because of the massive development of the cephalic capsule. This has had a disadvantageous effect on the taxonomy of the group since the shape of the capsule and the distribution and shape of the various locules which are frequently present have been used to delimit a large number of species. Filipjev (1916) and Wieser (1953) both report specimens, otherwise typical *T. articum*, in which no locules are present and Mawson (1956) points out that " the exact shape, and the number of loculi, are often subject to individual variation ". However no-one has previously studied the variation in the form of the locules in the entire capsule in a number of specimens, although Mawson (1958a) gives a dorsal, ventral and lateral view for the species she describes. I have studied the form of the posterior part of the capsule in detail in the three species I describe below, and its structure is illustrated in Text-figs. 148, 159–162, 163–166 and 177–179. Each figure represents the capsule of one specimen with the dorsal lobe in the centre, the right dorso-lateral, the right ventro-lateral and the ventral lobes drawn to the right and the left dorso-lateral, the left ventro-lateral and the ventral lobes drawn to the left. That is, the ventral lobe is shown twice, on the extreme right and left of the strip. Each figure represents a compilation from twelve separate figures—one for each sector of the capsule and one for each incision. The distribution of the nuchal setae is also shown. One thing is immediately obvious from the figures, there is no sexual dimorphism. Secondly, the number of locules is of no value nor is their detailed shape. These factors vary too much, but certain conclusions can be drawn. The locules are simpler in the larvae and their size and number tends to increase in the adults. This increase in size, to the point where the locules fuse, is most spectacular in *T. zeae* (Text-figs. 177–179) but the same tendency is seen in *T. jae* (Text-figs. 159–166). The locules seem to follow a fairly definite pattern in the two species considered in detail here but I suspect that this would be of very little value if more species were taken into consideration. Nevertheless, the capsule has a characteristic appearance in all three species. This is largely a reflection of the length of the capsule from the anterior edges of the lacunae to the posterior edge of the capsule, the shape of the fenestrae and the width of the incisions. The distribution of the nuchal setae is also probably of some value but only those on the lateral aspect where they tend to occur in groups just posterior to the amphidial incision. I suspect that this also will break down when a wide range of species has been studied. The best characters still appear to be those afforded by the buccal armature—probably at a generic level—while the form of the male reproductive apparatus supplies very valuable characters for the delimitation of species. While the argument that characters are most useful when they allow both sexes to be separated has some validity it is unfortunately true that in many groups of nematodes it is extremely difficult, if not impossible, to separate females and the form of the gubernaculum in this genus appears to be particularly valuable in separating males. Many of the figures which have been published of the spicules and gubernaculum are quite insufficient by any standards and the real value of the variation of this set of organs cannot at present be assessed. In future descriptions attention must be paid not only to the form of the buccal armature—as has been stressed by Wieser (1956) and Mawson (1958a)—but also to the structure of the gubernaculum, in particular, and spicules. The importance of the presence or absence of a distal spine on the gubernaculum is uncertain since it appears either to vary in its occurrence or to be extremely difficult to find in some specimens and I would not recognize its absence as being of any significance.

Thoracostoma angustifissulatum Mawson, 1956
(Text-figs. 148–151)

MATERIAL STUDIED. 1 ♂. 32° 16′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. No. 1963. 21.

Ratios

a	*b*	*c*	*Body Length (mm.)*
42·9	5·1	69·8	9·0

MEASUREMENTS (in mm.). Body breadth : 0·21. Oesophagus length : 1·76. Cephalic capsule, depth/diameter at posterior edge : 0·042/0·060. Distance of nerve ring from anterior end of body : 0·54. Distance of eye spots from anterior end of body : 0·159. Tail length : 0·129. Cloacal diameter : 0·186. Spicule length :

0·213. Gubernaculum length : 0·148. Distance of pre-cloacal supplement anterior to cloacal opening : 0·114.

The head is exactly as described by Mawson (1956) which is the same as that of *T. jae* (see page 333). The posterior edge of the capsule is somewhat incised and the lacunae pierce each lobe relatively far anterior to the posterior edge of the capsule, roughly half-way between that edge and the level of the cephalic setae (Text-fig. 148). This also is stressed by Mawson. I have been unable to see any nuchal setae but Mawson points out that they are small and sparse in her specimens. There are paired eye spots with lenses.

The tail is very short and stout with the papillate pre-cloacal supplement lying relatively close to the cloacal opening. Anterior to the supplement are five pairs of papillae. The spicules are massive terminating distally in sharpish points. The gubernaculum is large with a distal process and a massive rounded proximal end. The distal end of the gubernaculum is blunt (Text-fig. 151).

DISCUSSION

Mawson records this species from many Arctic and Subantarctic localities. For details reference should be made to the original publications, Mawson : 1956, 1958, 1958a. The species is characterized by the form of the mouth armature, the length of the cephalic capsule, the occurrence of the lacunae of the capsule relatively far anterior to the posterior edge, and the massive form of the gubernaculum.

Thoracostoma jae sp. nov.

(Text-figs. 152–166)

Material Studied. 6 ♂♂ (1 selected as holotype), 5 ♀♀, 5 larvae. 32° 06′ S./ 18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 166–179 (1 ♂, 1 ♀ returned to South Africa).

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	35·4	5·1	65·8		6·7
	35·5	5·0	69·8		7·1
	31·3	4·9	61·5		7·2
	38·0	5·3	74·3		7·6
	39·5	5·7	79·0		8·3
	44·0	5·4	76·5		8·8
Females	29·6	5·0	79·6	66·2	7·4 (? 4th-larva)
	33·7	5·5	79·2	62·0	8·4
	34·6	5·7	78·9	64·4	9·0
	40·0	5·5	82·1	61·9	9·2
	42·8	5·7	83·2	62·8	9·4
Larvae	23·3	3·6	48·6		3·5
	34·6	4·0	47·0		3·8
	30·0	5·3	74·2		6·9

Measurements (in mm. in order of body lengths above). *Males.* Body breadth : 0·19 ; 0·20 ; 0·23 ; 0·20 ; 0·21 ; 0·20. Oesophagus length : 1·33 ; 1·43 ; 1·46 ;

1·44 ; 1·46 ; 1·62. Cephalic capsule, depth/diameter at posterior edge : 0·032/0·058 ; 0·039/0·060 ; 0·036/0·060 ; 0·039/0·057 ; 0·036/0·057 ; 0·039/0·057. Distance of nerve ring from anterior edge of body : 0·43 ; 0·45 ; 0·47 ; 0·47 ; 0·49 ; 0·50. Distance of eye spots from anterior end of body : 0·126 ; 0·138 ; 0·132 ; 0·120 ; 0·123 ; 0·132. Tail length : 0·102 ; 0·102 ; 0·117 ; 0·102 ; 0·105 ; 0·114. Cloacal diameter : 0·116 ; 0·120 ; 0·141 ; 0·138 ; 0·156 ; 0·132. Spicule length : 0·149 ; 0·165 ; 0·153 ; 0·162 ; 0·156 ; 0·144. Gubernaculum length : 0·113 ; 0·119 ; 0·112 ; 0·122 ; 0·116 ; 0·114. Distance of pre-cloacal supplement anterior to cloacal opening : 0·099 ; 0·121 ; 0·109 ; 0·097 ; 0·111 ; 0·120. Number of pairs of ventro-lateral papillae anterior to pre-cloacal supplement : 6, 6, 5, 7, 6, 5.

Females. Body breadth : 0·25 ; 0·25 ; 0·26 ; 0·23 ; 0·22. Oesophagus length : 1·48 ; 1·53 ; 1·57 ; 1·68 ; 1·66. Cephalic capsule, depth/diameter at posterior edge : 0·029/0·057 ; 0·033/0·057 ; 0·042/0·063 ; 0·048/0·063 ; 0·049/0·061. Distance of nerve ring from anterior end of body : 0·49 ; 0·48 ; 0·50 ; 0·54 ; 0·49. Distance of eye spots from anterior end of body : 0·126 ; 0·138 ; 0·135 ; 0·132 ; 0·129. Tail length : 0·093 ; 0·106 ; 0·114 ; 0·112 ; 0·113. Anal diameter : 0·112 ; 0·120 ; 0·134 ; 0·120 ; 0·131. Distance of vulva from anterior end of body : 4·9 ; 5·2 ; 5·8 ; 5·7 ; 5·9. The eggs are 0·387 × 0·150 ; 0·344 × 0·174 ; 0·288 × 0·180 ; 0·393 × 0·138.

Larvae. Body breadth : 0·15 ; 0·11 ; 0·23. Oesophagus length : 0·97 ; 0·95 ; 1·30. Cephalic capsule, depth/diameter at posterior end : 0·027/0·039 ; 0·033/0·045 ; 0·029/0·051. Distance of nerve ring from anterior end of body : 0·36 ; 0·35 ; 0·44. Distance of eye spots from anterior end of body : 0·099 ; 0·114 ; 0·123. Tail length : 0·072 ; 0·081 ; 0·093. Anal diameter : 0·078 ; 0·078 ; 0·114.

The head carries a bifid onchium on the dorsal side of the mouth cavity and two thinner but similar bifid-structures on each ventro-lateral side of the mouth cavity (Text-figs. 157 and 158). The cephalic capsule is relatively short with narrow incisions and an irregular posterior edge. The fenestration lies near the posterior edge of the capsule and when extensive takes the form of long narrow fenestrae or several small circular fenestrae (Text-figs. 159–166). The nuchal setae tend to form single files on the dorso- and ventro-lateral sectors and to occur in groups of five or six, followed by single files, posterior to the amphids.

The spicules are rather lightly built, the gubernaculum is slim and no distal lateral processes were seen (Text-fig. 155). There are five to seven pairs of papillae anterior to the pre-cloacal supplement the occurrence of which is detailed above. The testes are opposed.

DISCUSSION

This species appears to be, on the basis of the form of the cephalic capsule, close to *Thoracostoma antarcticum* (von Linstow, 1892) and, to a lesser extent, on the form of the spicules but differs from it in the lightly built gubernaculum—and the lighter build of the spicules. It is also similar to *T. steineri* Micoletzky, 1922 in the light build of the spicules and gubernaculum but is totally different from it in the form of the cephalic capsule.

Thoracostoma zeae sp. nov.
(Text-figs. 167–179)

Material Studied. 1 ♂ (holotype), 3 larvae. 32° 06′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 133–136.

	Ratios			
	a	*b*	*c*	*Body Length (mm.)*
Male	32·5	6·6	74·3	10·4
Larvae	32·6	5·5	76·9	6·0
	40·5	5·6	76·0	7·3
	46·8	4·2	72·3	8·9

Measurements (in mm. in order of body lengths above). *Male.* Body breadth : 0·32. Oesophagus length : 1·58. Cephalic capsule, depth/diameter at posterior edge : 0·030/0·066. Distance of nerve ring from anterior end of body : 0·51. Distance of eye spots from anterior end of body : 0·114. Tail length : 0·14. Cloacal diameter : 0·20. Spicule length : 0·28. Gubernaculum length : 0·18. Distance of pre-cloacal supplement anterior to cloacal opening : 0·13. Distance of first/second pair of papillae anterior to cloacal opening : 0·26/0·44.

Larvae. Body breadth : 0·19 ; 0·18 ; 0·19. Oesophagus length : 1·09 ; 1·30 ; 1·67. Cephalic capsule, depth/diameter at posterior edge : 0·027/0·048 ; 0·027/0·056 ; 0·027/0·060. Distance of nerve ring from anterior end of body : 0·354 ; 0·410 ; 0·396. Distance of eye spots from anterior end of body : 0·090 ; 0·090 ; 0·111. Tail length : 0·078 ; 0·096 ; 0·123. Anal diameter : 0·108 ; 0·129 ; 0·150.

The head has a large onchium in the centre of each ventro-lateral lobe of the mouth cavity but not on the dorsal (Text-fig. 171). The cephalic capsule is short with very wide incisions and a very irregular posterior edge. The fenestrations lie very near the posterior edge and on elaborating tend to increase in size and then to pierce the posterior edge (see Text-figs. 177–179). The nuchal setae are restricted to groups of four to six just posterior to the amphids. There are no long files of setae as in the other species described here. The frame-work of the amphids is very prominent and projects posteriorly as a square ended mass which occupies most of the space of the amphidial incisions. The eye spots are typical with prominent lens.

The male tail carries the usual median papilloid pre-cloacal supplement anterior to which are only two pairs of ventro-lateral papillae. Between the pre-cloacal supplement and the cloacal opening are a number of long ventro-lateral setae, with a series of short setae lying close together just anterior to the cloacal opening. The spicules are narrow proximally but broaden rapidly distal to the bend (Text-fig. 174 and 175). The gubernaculum is blunt both proximally and distally and is about the same width along its whole length. There is a stout lateral terminal process (Text-fig. 174).

DISCUSSION

This species is very distinctive in the massive breakdown of the cephalic capsule by the multiplication, extension and fusion of the lacunae and the form and position of the amphids. It is further characterized by, so far as it is possible to confirm this character, the form of the lip dentition, the presence of only two pairs of pre-cloacal papillae, the even thickness of the gubernaculum and, possibly, by the form of the spicules. It is perhaps most similar to *T. zolae* Marion, 1870 and *T. steineri* Micoletzky, 1922 but differs in the massive lacunation of the cephalic capsule, the form of the gubernaculum and in possessing only two pre-cloacal papillae. (See Schuurmans Stekhoven, 1943).

Family **ENCHILIDIIDAE** Micoletzky, 1924
Eurystomina Filipjev, 1918

This genus has been reviewed elsewhere and will not be discussed further here (Inglis, 1962).

Eurystomina sudensis sp. nov.
(Text-figs. 180–183)

Material Studied. 1 ♂ (holotype) and two very poorly preserved specimens, 1 ♂, 1 ♀. 32° 05′ S./18° 16′ E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. No. 1963. 45.

Ratios

a	*b*	*c*	*Body Length* (*mm.*)
186·0	6·9	62·9	8·1

Measurements (mm.). Body breadth : 0·069. Oesophagus length : 1·17. Excretory pore immediately posterior to head. Cephalic setae, long/short : 0·019/0·005. Diameter of head : 0·034. Depth of buccal cavity : 0·030. Diameter of buccal cavity at level of denticles : 0·017. Length of longest tooth : 0·022. Tail length : 0·129. Cloacal diameter : 0·060. Spicule length : 0·066. Gubernaculum length : 0·034. Distance of 1st pre-cloacal supplement anterior to cloacal opening : 0·18. Distance of 2nd supplement anterior to first : 0·14.

This species is absolutely typical of the genus *Eurystomina* with the left ventro-lateral tooth the longest and with two rows of denticles in the mouth cavity except at the point opposite the longest onchium where there are three (Text-figs. 180 and 181). The spicules are short and fairly stout without dentate processes on the distal ends. The gubernaculum is simple and non-fenestrate with a small rounded apophysis (Text-fig. 182). The tail is short and stout (Text-fig. 183).

DISCUSSION

E. sudensis is characterized by the short, stout spicules, the short tail and the relatively small, simple gubernaculum.

Family **ONCHOLAIMIDAE** Micoletzky, 1922

Pontonema Leidy, 1855

Pontonema yaenae sp. nov.

(Text-figs. 184–188)

MATERIAL STUDIED. 10 ♂♂ (1 selected as holotype), 5 ♀♀, 3 larvae. 32° 02′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 91). B.M. (N.H.), Reg. Nos. 1963. 142–157. (1 ♂, 1 ♀ returned to South Africa).

2 ♂♂, 2 ♀♀ (+ 2 ♂♂, 1 ♀, 2 larvae in very poor condition). 32° 06′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 158–165.

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	50·9	7·3	46·9		6·1
	58·2	7·1	45·7		6·4
Females	43·0	6·5	46·0	43·5	6·9
	41·8	6·8	41·7	47·9	7·1

MEASUREMENTS (in mm., in order of body lengths above). *Males.* Body breadth : 0·12 ; 0·11. Oesophagus length : 0·83 ; 0·91. Distance of nerve ring from anterior end of body : 0·36 ; 0·38. Distance of excretory pore from anterior end of body : 0·046 ; 0·048. Diameter of head : 0·054 ; 0·060. Length of cephalic setae, long/short ; 0·014/0·010 ; 0·016/0·012. Buccal cavity, length/breadth : 0·093/0·036 ; 0·105/0·032. Tail length : 0·13 ; 0·14. Cloacal diameter : 0·064 ; 0·072. Length of spicules : 0·073 ; 0·072. Length of gubernaculum (= apophysis) : 0·041 ; 0·048.

Females. Body breadth : 0·16 ; 0·17. Oesophagus length : 1·06 ; 1·04. Distance of nerve ring from anterior end of body : 0·41 ; 0·43. Distance of excretory pore from anterior end of body : 0·050 ; 0·052. Diameter of head : 0·063 ; 0·064. Length of cephalic setae, long/short : 0·012/0·011 ; 0·012/0·010. Buccal cavity ; length/breadth : 0·114/0·039 ; 0·116/0·042. Tail length : 0·15 ; 0·17. Anal diameter : 0·075 ; 0·079. Distance of vulva from anterior end of body : 3·0 ; 3·4. Eggs are about 0·32 × 0·11 in size.

The head is typical with a large buccal cavity in which the dorsal onchium is smaller than the two equal ventro-lateral onchia and lies far posterior (Text-figs. 184 and 185). The amphids are prominent and the large semi-lunar openings lead into circular pouches (Text-fig. 185). There are several small setae on the body between the level of the amphids and the opening of the excretory pore which do not appear to follow a fixed pattern. The tail is short and stout in both sexes (Text-fig. 186).

The male tail bears a series of long, stout setae in two rows on the ventro-lateral surfaces and there is a similar series extending anteriorly from the cloacal opening. There are no pre-cloacal papillae. The spicules are simple in outline and the gubernaculum bears a distinct apophysis which is enlarged distally to enfold the spicules. This enlarged zone is pierced by a large circular hole (Text-fig. 188).

DISCUSSION

Kreis' (1934a) key has been modified and brought up to date by Mawson (1956) but I am not happy about keys based on ratios which lie as close together as, for example, Tail 1·5–2 × anal breadth and Tail 1–1·5 × anal breadth, particularly in a group such as this in which the tail tends to be strongly curled ventrally. If Mawson's key is used this species comes down to *Pontonema brevicaudatus* (Menzel, 1920) from which it differs markedly in lacking papillae on the male tail. It appears also to be similar in general appearance to *P. macrolaimus* (Southern, 1914), *P. parpapilliferus* Micoletzky, 1924 and *P. papilliferus* Filipjev, 1916 in the location of the dorsal onchium within the onchial cavity and the short tail but differs from all three species in the slim gubernaculum with its fenestrate distal end and in not possessing pre-cloacal papillae.

Family **IRONIDAE** de Man, 1876

Thalassironus de Man, 1889

Thalassironus jungi sp. nov.

(Text-figs. 189–194)

Material Studied. 3 ♂♂ (1 selected as holotype), 11 ♀♀, 5 larvae (mostly very coiled). 32° 05′ S./18° 16′ E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. Nos. 1963. 22–38. (1 ♂, 1 ♀ returned to South Africa).

2 ♂♂, 1 ♀. 32° 05′ S./18° 17′ E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 93). B.M. (N.H.), Reg. Nos. 1963. 39–41.

	Ratios				
	a	*b*	*c*	*V*	*Body Length (mm.)*
Males	63·3	7·4	26·9		5·0
	65·4	7·5	28·2		5·3
	66·3	7·6	28·2		5·5
	65·5	7·3	27·9		5·7
Females	64·4	8·6	30·9	57·1	5·6
	63·7	9·4	31·7	58·6	5·8

Measurements (in mm. in order of body lengths above). *Males.* Body breadth : 0·079 ; 0·081 ; 0·083 ; 0·087. Oesophagus length : 0·68 ; 0·71 ; 0·72 ; 0·78. Diameter of head : 0·028 ; 0·034 ; 0·032 ; 0·035. Length of cephalic setae, long/short : 0·026/0·014 ; 0·027/0·015 ; 0·027/0·016 ; 0·027/0·016. Length of paired cervical setae : 0·026 ; 0·025 ; 0·026 ; 0·026. Diameter of body at level of cervical setae : 0·048 ; 0·047 ; 0·048 ; 0·049. Length of pharyngeal rods : 0·097 ; 0·101 ; 0·098 ; 0·099. Distance of nerve ring from anterior end of body : 0·24 ; 0·23 ; 0·26 ; 0·26. Tail length : 0·186 ; 0·188 ; 0·195 ; 0·204. Cloacal diameter : 0·066 ; 0·067 ; 0·070 ; 0·069. Spicule length : 0·060 ; 0·058 ; 0·060 ; 0·060. Gubernaculum length : 0·030 ; 0·030 ; 0·028 ; 0·029.

Females. Body breadth : 0·087 ; 0·091. Oesophageal length : 0·65 ; 0·62. Diameter of head : 0·035 ; 0·036. Length of cephalic setae, long/short : 0·034/0·016 ; 0·034/0·014. Length of paired cervical setae : 0·027/0·029. Diameter of body at level of cervical setae : 0·049 ; 0·046. Length of pharyngeal rods : 0·074 ; 0·076. Distance of nerve ring from anterior end of body : 0·27 ; 0·25. Tail length : 0·181 ; 0·183. Anal diameter : 0·059 ; 0·062. Distance of vulva from anterior end of body : 3·2 ; 3·4.

The head is similar in structure of that of *Trissonchulus janetae* Inglis, 1961 differing only in the presence of long cephalic setae (Text-figs. 189 and 192). There are two small paired solid cuticular onchia on the anterior end of the dorsal sector of the oesophagus and one large onchium on each ventro-lateral sector (Text-fig. 190). The cephalic setae lie in an outer circle and six are longer than the remaining four. The inner circle of labial sense organs is composed of six sessile papillae. There is a distinct cephalic capsule on the posterior edge of which lie the openings of the amphids which lead into large pockets (Text-fig. 189). Immediately posterior to each amphid is a doubled seta. This large structure appears at first to consist of two setae but the two components appear to be separate at the distal end only. In all the larvae there is a set of secondary teeth near the anterior end of the oesophagus (Text-fig. 193).

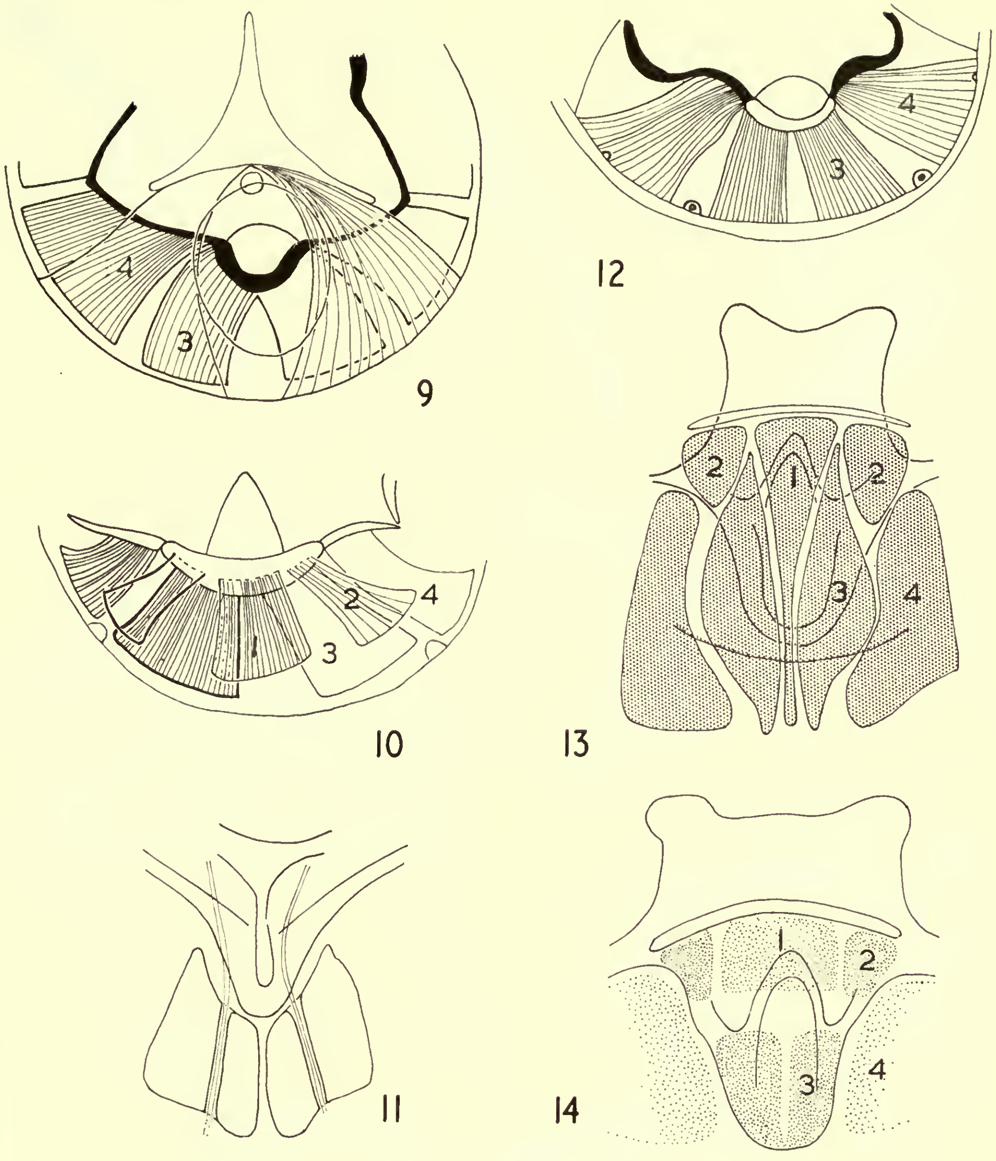
The tail is the same shape in both sexes (Text-fig. 194) and the caudal glands lie anterior to the cloacal or anal opening. In the male there is no pre-cloacal modification, the spicules are short and massive with bluntly capitate proximal and sharply pointed distal ends. The gubernaculum is small with a thin proximal end and stout distal end (Text-fig. 191). The testes are paired and opposed just as in *T. janetae*. Similarly the reproductive system of the female consists of two opposed uteri and associated reflexed ovaries, with very large eggs, 0·378 × 0·076 to 0·420 × 0·083 mm.

DISCUSSION

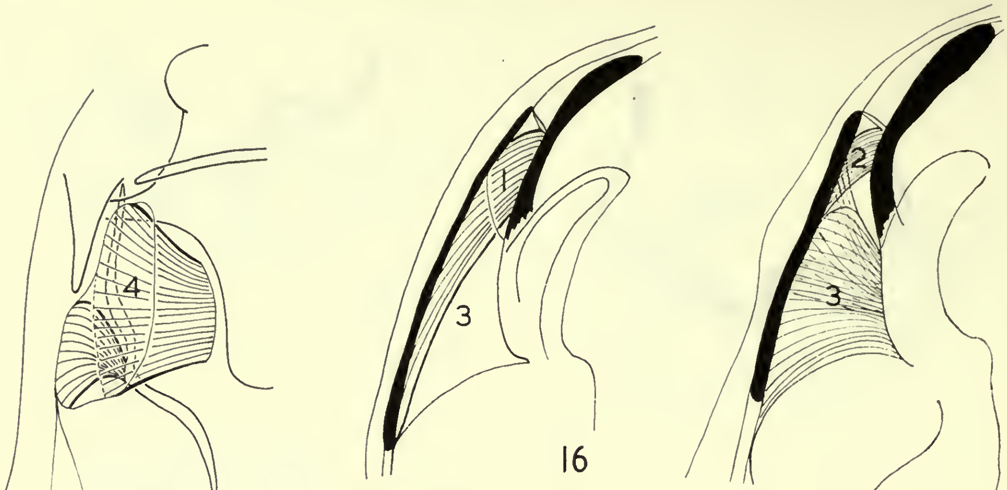
Currently the genus *Thalassironus* contains only two species, *T. britannicus* de Man, 1889 (recently redescribed from the types by Chitwood, 1960) and *T. bipartitus* (Wieser, 1953) (originally referred to *Parironus* Micoletzky, 1930 but transferred to *Thalassironus* by Chitwood (1960)). The present species differs from both these in the presence of the long " double " cervical setae, the great length of the cephalic setae and in the form of the spicules and gubernaculum.

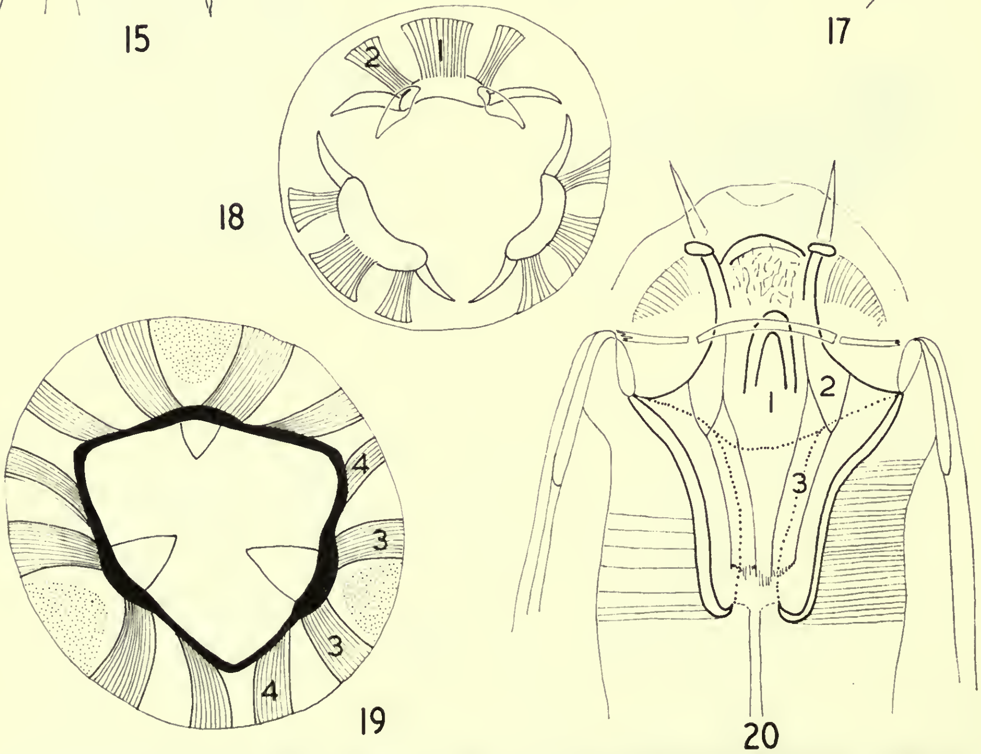
Text-figures 9-194

and References



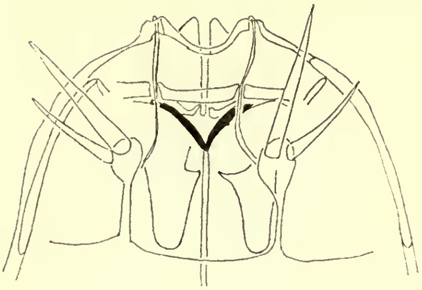
Figs. 9–14. *Mesonchium studiosa.* Fig. 9. Transverse section cut just posterior to onchium looking anteriorly showing general musculature of oesophagus, duct of oesophageal gland, the sudden expansion of the onchial cavity and the distribution of muscles-3 and -4. Fig. 10. *En face* view of distribution of oesophageal musculature. Fig. 11. View taken at end of a radius of the oesophagus showing distribution of origins of Muscles-4 and nerves to labial sense organs. Fig. 12. Transverse section just about mid-level of onchial plate. Fig. 13. Origins of oesophageal musculature. Fig. 14. Areas of insertion of musculature on onchial plate and flanking lining of oesophageal radii.





FIGS. 15–17. *Mesonchium studiosa.* Fig. 15. Distribution of Muscle-4. Fig. 16. Longitudinal section through head showing longitudinal distribution of Muscles-1 and -3. Fig. 17. The same showing distribution of Muscles-2 and -3. Note that the more lateral parts of Muscle-3 are directed posteriorly while the median part is fanned anteriorly.

FIGS. 18–20. *Enoplolaimus mus.* Fig. 18. *En face* view of distribution of anterior ring of oesophageal muscles (compare with Fig. 10). Fig. 19. Transverse section about level of origin of onchium. Fig. 20. Origins of oesophageal musculature.



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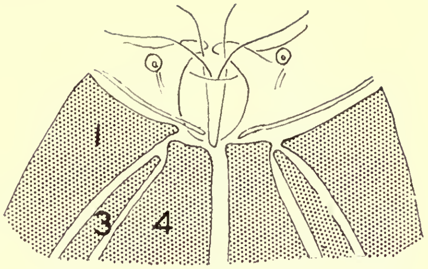

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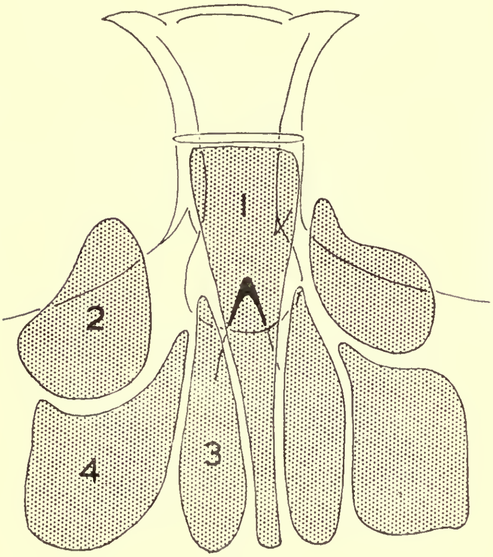

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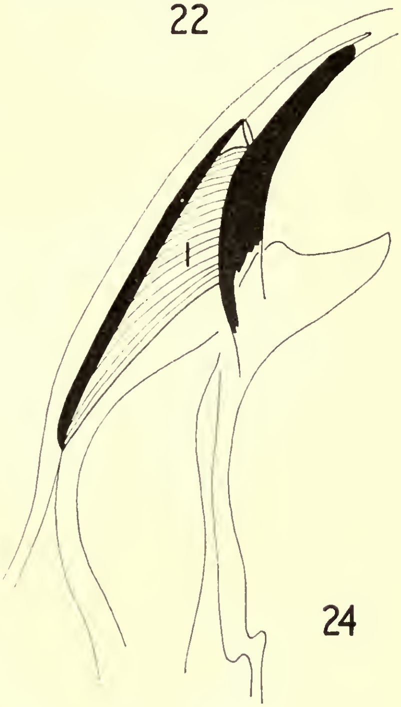

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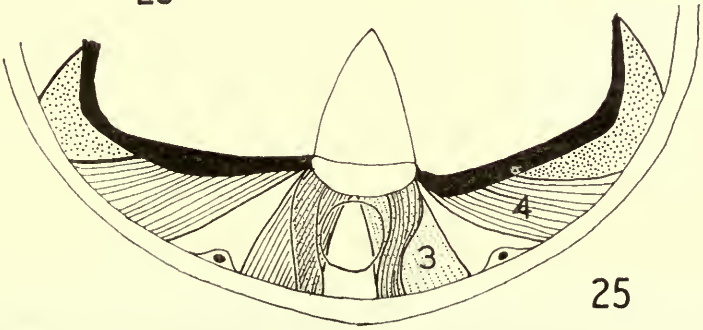

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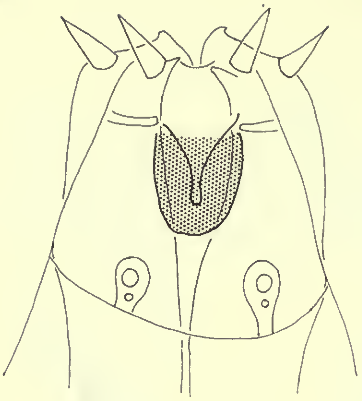
FIGS. 21 and 22. *Enoplus harlockae.* Fig. 21. View taken at end of a radius of oesophagus showing distribution of nerves to labial sense organs and the position of the radial process (solid black) relative to the cephalic ring. Fig. 22. Distribution of muscle origins at a radius.

FIGS. 23–25. *Africanthion nudus.* Fig. 23. Origins of oesophageal musculature. Fig. 24. Longitudinal section through one lip showing distribution of Muscle-1. Fig. 25. Transverse section just posterior to onchium showing very narrow general oesophageal musculature enfolding oesophageal gland duct, the distribution of Muscles-3 and -4 and the massive radial process (stippled).



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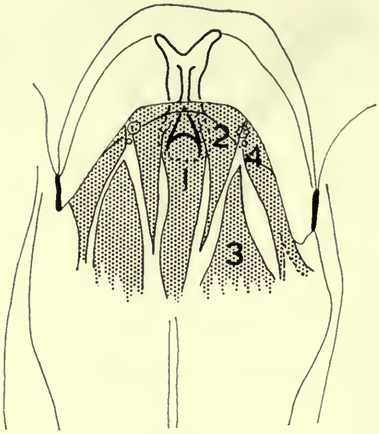

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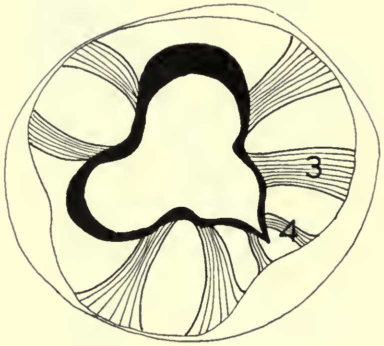

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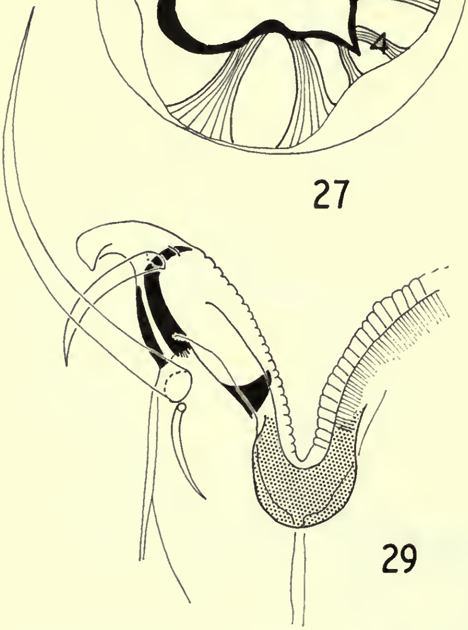

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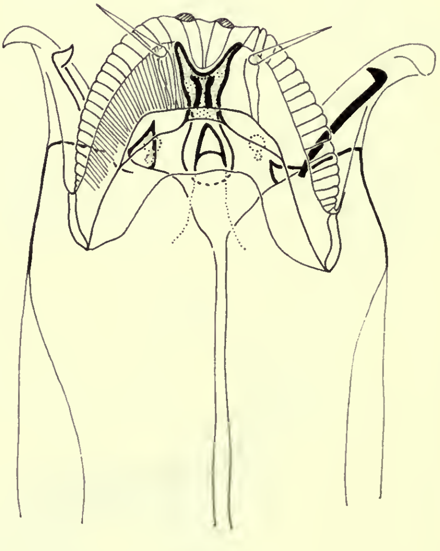

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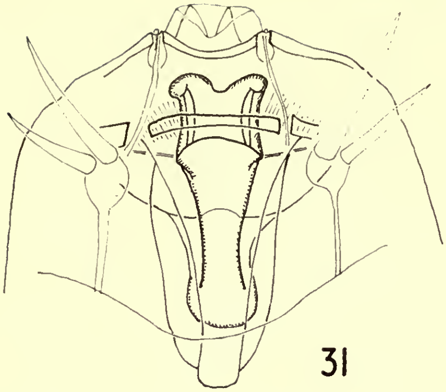
FIGS. 26 and 27. *Trileptium ayum*. Fig. 26. View taken at the end of a radius showing extensive radial mass (stippled) and the extreme posterior level at which the radial processes articulate relative to the cephalic ring. Fig. 27. Obliquely transverse section showing relatively small Muscles-4 and the way in which they disappear (upper left side of figure) before full development of onchium. (The section is cut more posteriorly on the lower right side of the figure.)

FIGS. 28–30. *Enoploides* sp. Fig. 28. Origins of oesophageal musculature. Note partial fusion of Muscles-1 and -2. Fig. 29. View taken at the end of one radius showing radial mass (stippled), striated outer rim to lips, light mandibles and supplementary strengthening structure in outer cuticle at same level as mandible. Fig. 30. Dorsal view of head.



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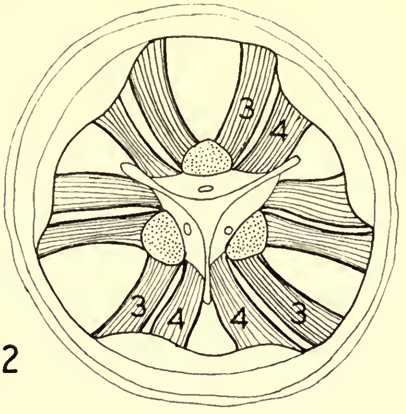

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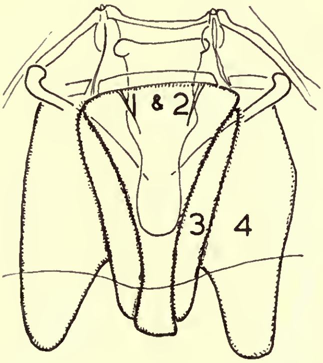

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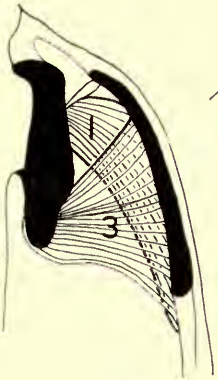

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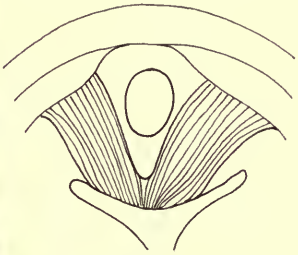

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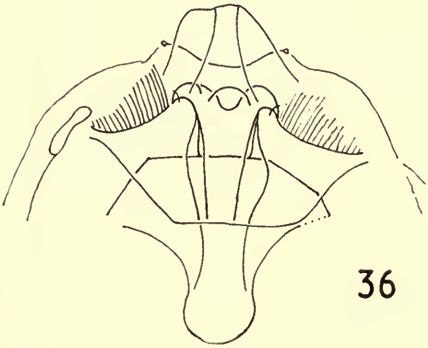

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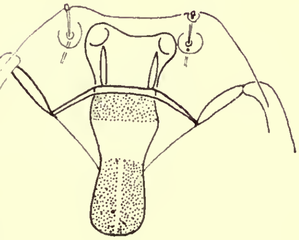

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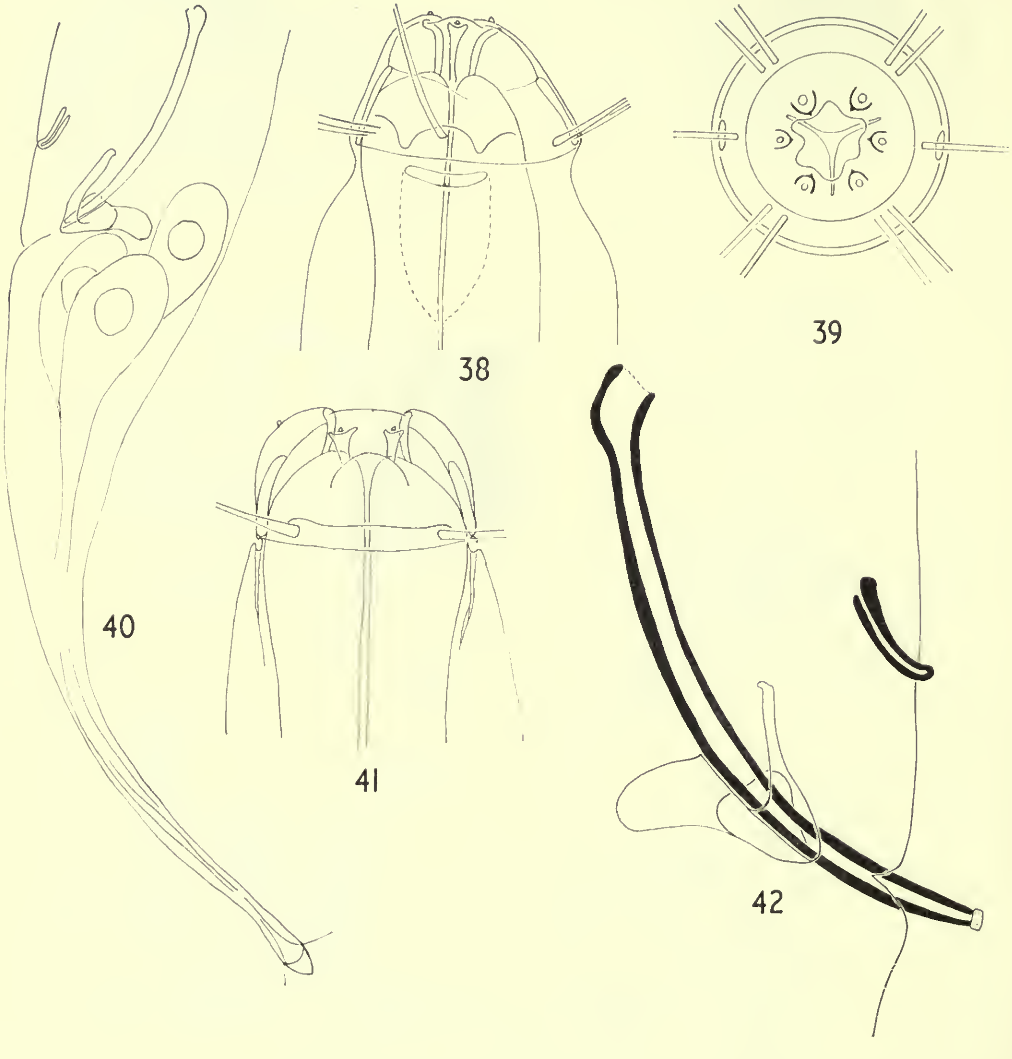
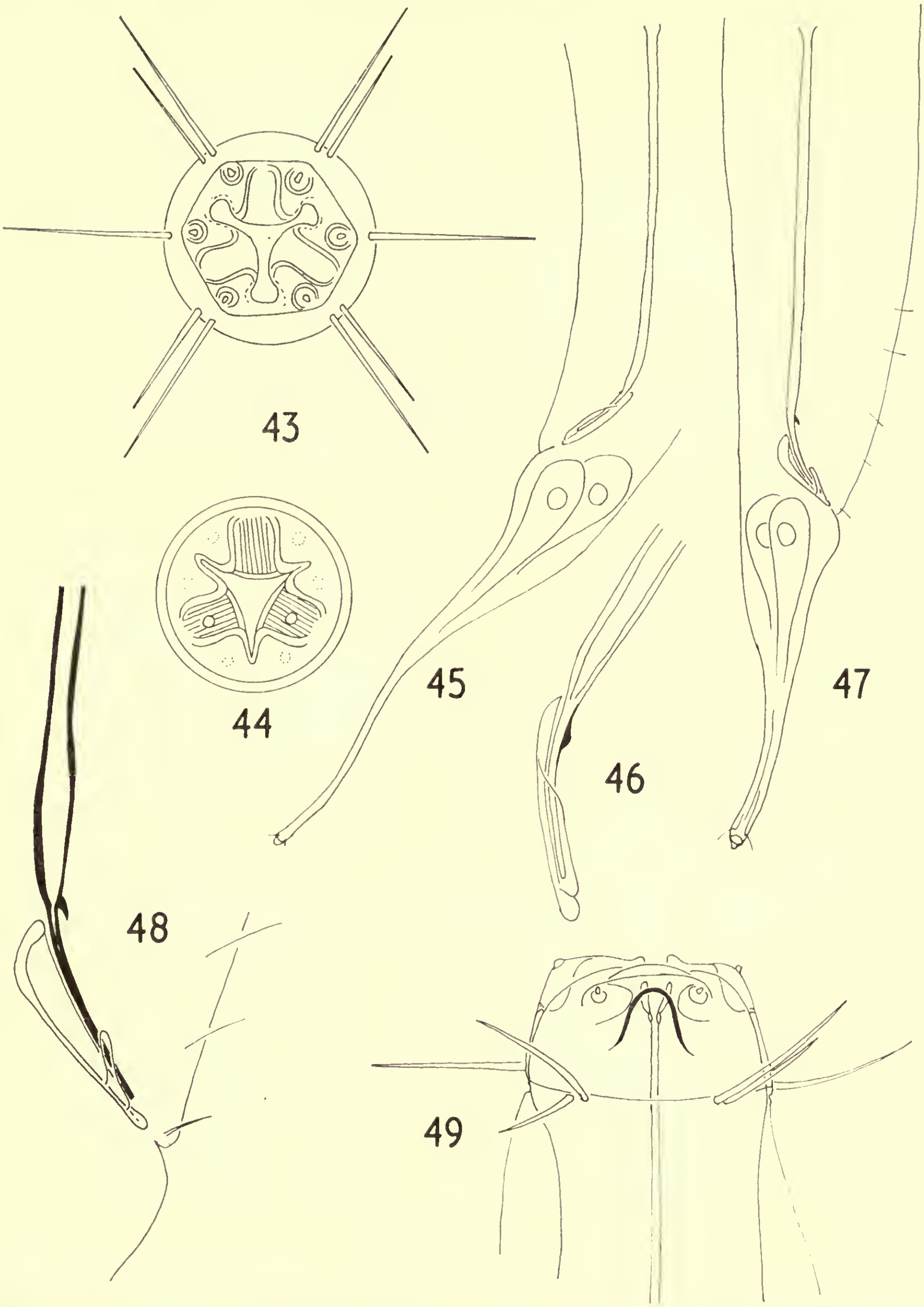
FIGS. 31–37. *Enoplus harlockae*. Fig. 31. Dorsal view of lip showing form of mandibular : onchial-plate complex. Fig. 32. Transverse section at level of posterior third of complex. Note attachment of oesophagus to body wall. Fig. 33. Origins of oesophageal musculature. Fig. 34. Longitudinal section showing distribution of Muscles-1 and -3. Fig. 35. Transverse section posterior to onchial complex showing distribution of general oesophageal musculature relative to duct of oesophageal gland. Fig. 36. Inner view of lip. Fig. 37. Exterior view of lip under pressure showing insertions of oesophageal musculature (stippled) and the form of the onchial plate, the mandibular ring and the radial masses.

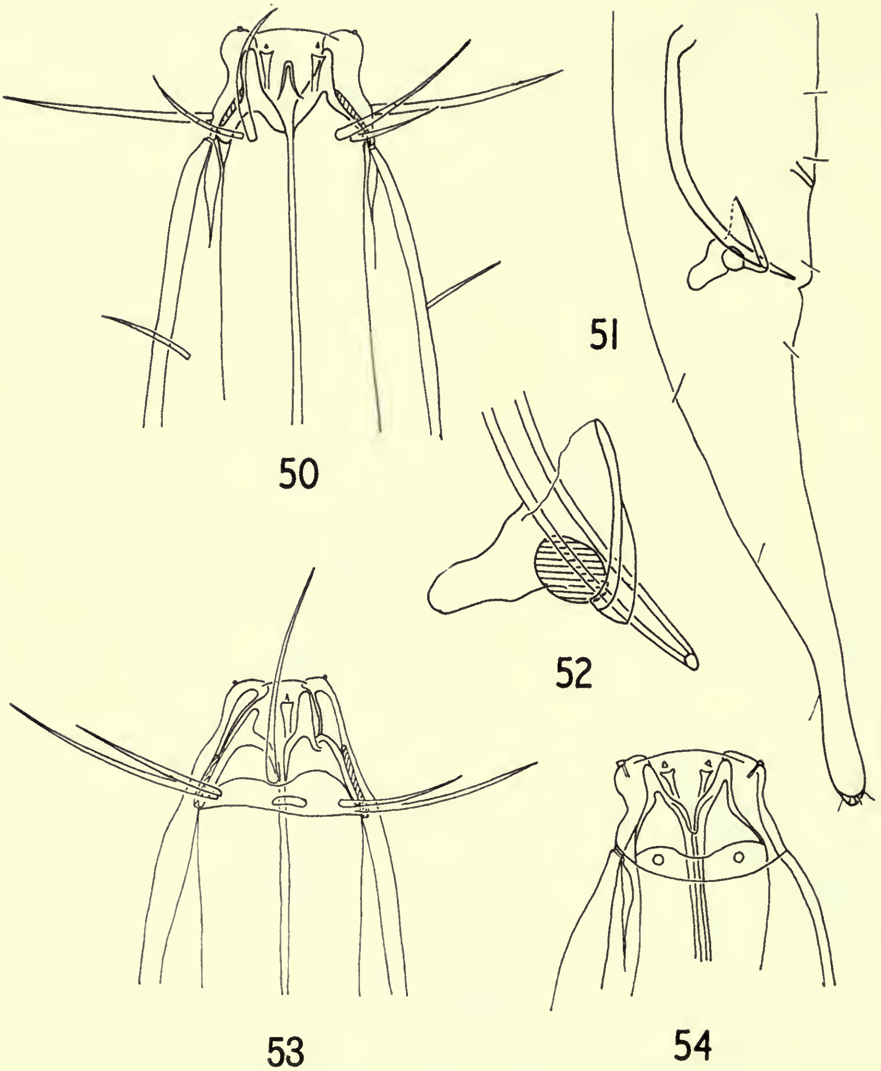


Figs. 38–42. *Dayellus dayi*. Fig. 38. Lateral view of head with dorsal surface to the left. Fig. 39. *En face* view of head. Fig. 40. Lateral view of male tail. Fig. 41. Dorsal view of head. Fig. 42. Detail of spicules and gubernaculum from the lateral aspect. Note particularly the square capped posterior end to the spicule.

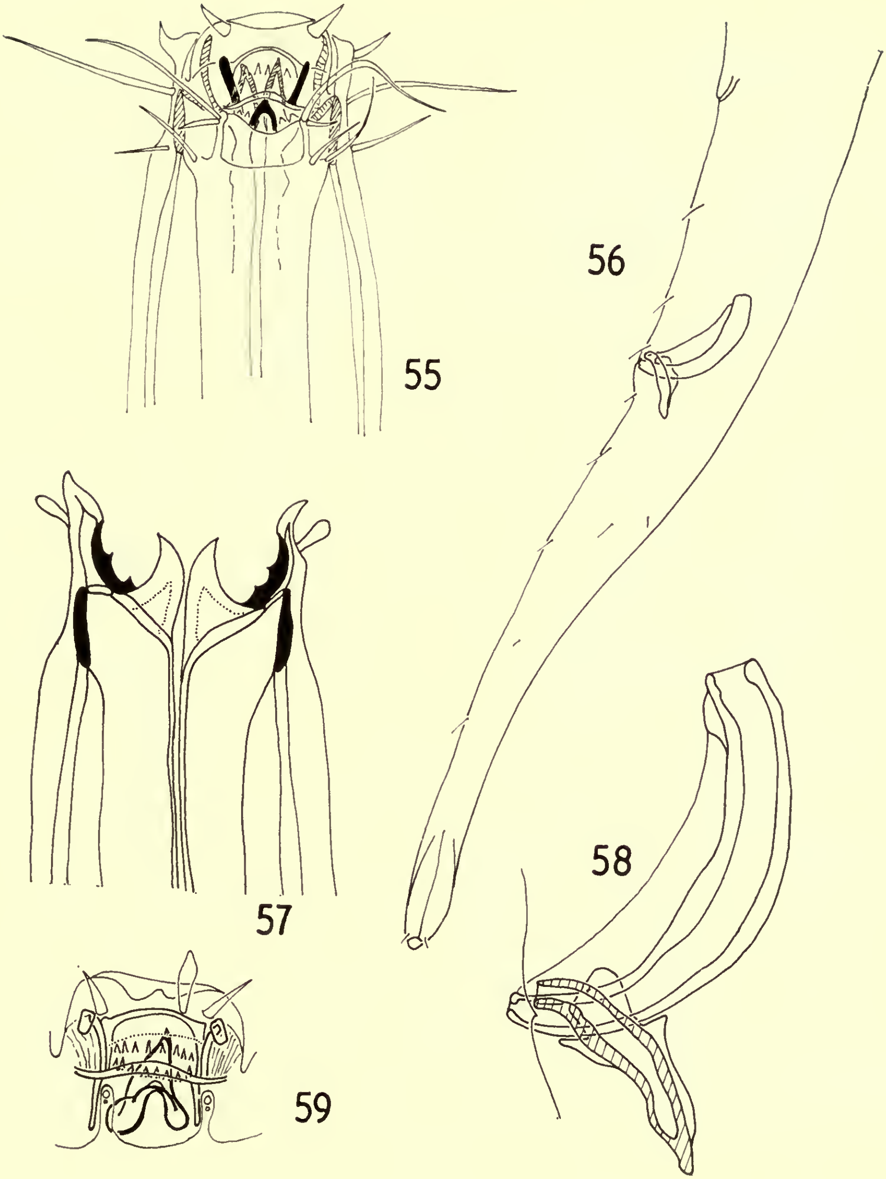


FIGS. 43, 44, 47–49. *Crenopharynx eina.* Fig. 43. *En face* view of head. Fig. 44. Deep *en face* optical section of head about level at which the three anterior prolongations of the oesophageal sectors separate. The solid circles are the ducts of the ventro-lateral oesophageal glands while the dotted circles represent the nerves which supply the labial sense organs. Fig. 47. Lateral view of male tail. Fig. 48. Detail of posterior end of spicules, showing large barb, and form of the gubernaculum. Fig. 49. Dorsal view of head.

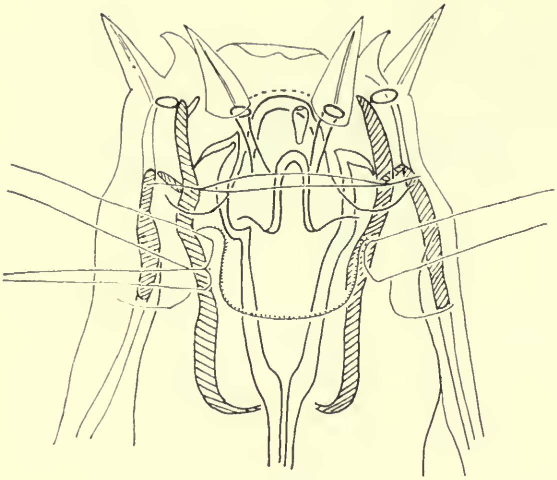
FIGS. 45–46. *Crenopharynx afra.* Fig. 45. Lateral view of male tail. Fig. 46. Detail



Figs. 50–54. *Phanoderma unica*. Fig. 50. Dorsal view of head. Fig. 51. Lateral view of male tail. Fig. 52. Detail of gubernaculum. Fig. 53. Lateral view of head with dorsal surface to the left. Fig. 54. Ventral view of head. Cephalic setae not drawn for clarity.



FIGS. 55–59. *Oxyonchus ditlevseni.* Fig. 55. Dorsal view of head. Fig. 56. Male tail from the lateral aspect. Fig. 57. Optical section through head, from dorsal surface, at level of cephalic cirri. Fig. 58. Detail of gubernaculum and spicules. Fig. 59. Detail of ventro-lateral lip, with dorsal surface to the right, showing distinct mandibular rods, cephalic cirrus and distribution of small denticles on inner surface of mandibular plate.



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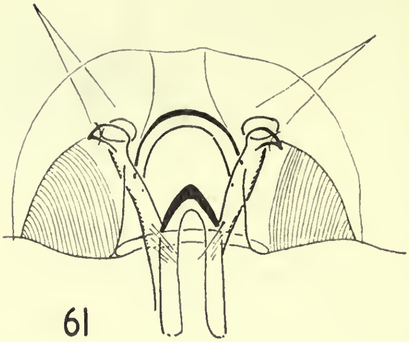

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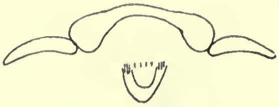

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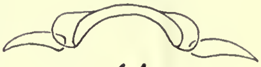

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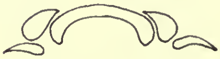

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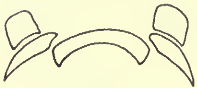

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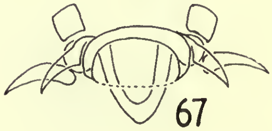

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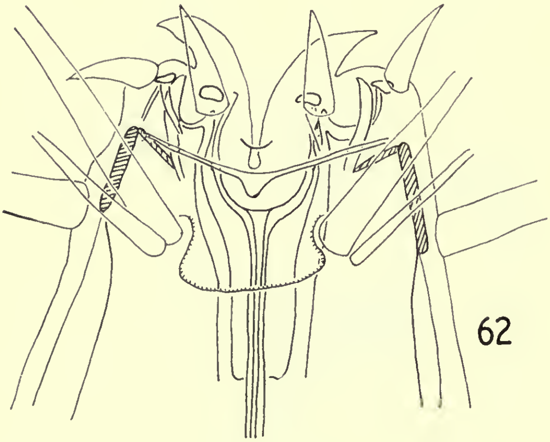

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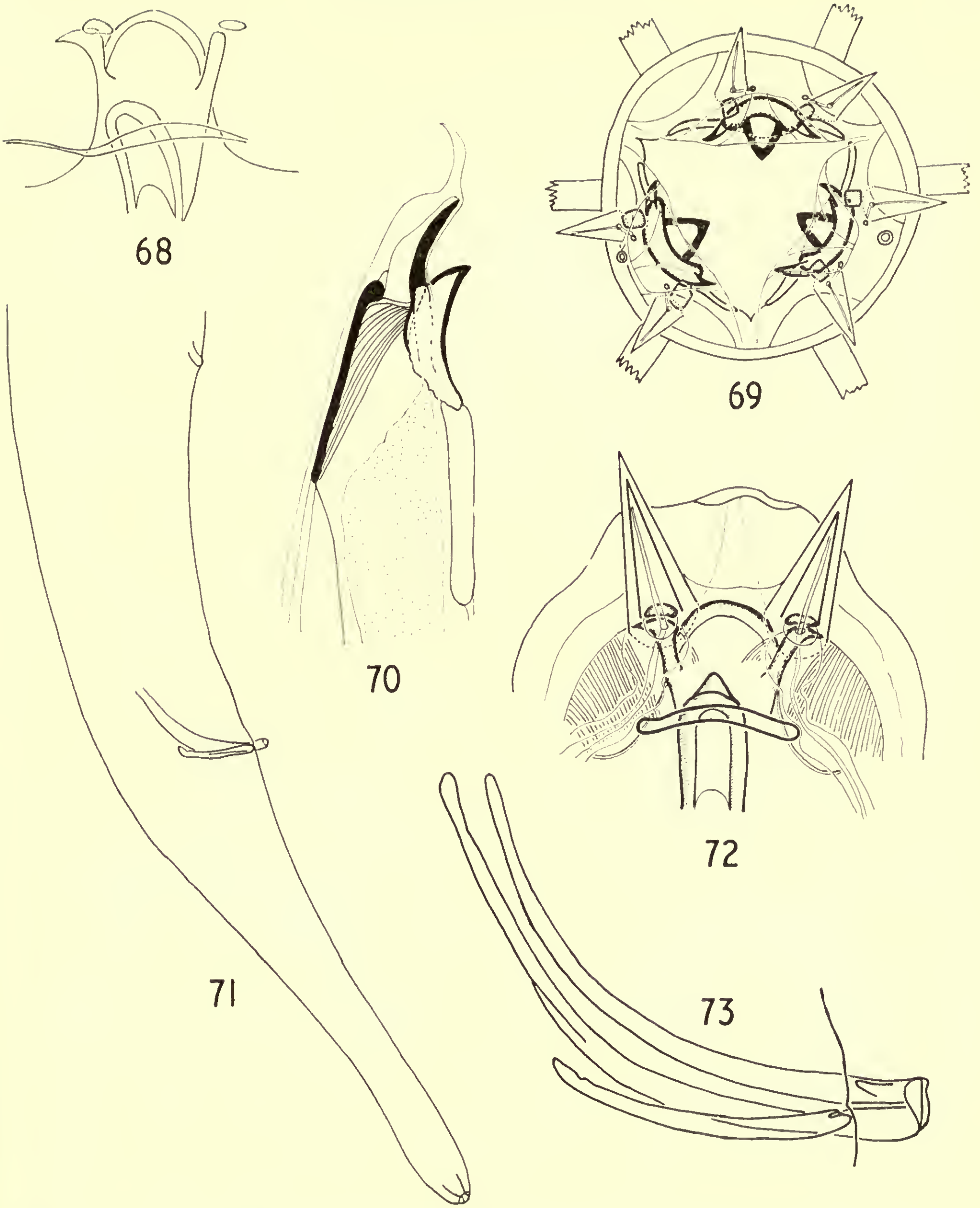
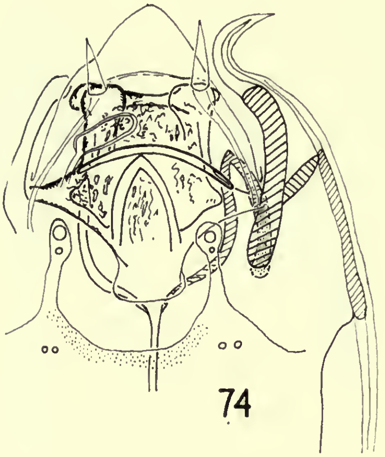
FIGS. 60–67. *Enoplolaimus mus* Fig. 60. Ventro-lateral view of head showing cephalic capsule and mandibular : onchial complex in optical section (cross-hatched). Fig. 61. View of lip from inner surface. Fig. 62. Ventral view of head. Figs. 63–66. Optical *en face* sections of mandibular : onchial-plate complex, from posterior end (63) anteriorly (66). Note separation of mandibular rods from mandibular plate at levels indicated in Figs. 64 and 65. Fig. 67. Composite *en face* view of complex.



FIGS. 68–73. *Enoplolaimus mus*. Fig. 68. Mandibular : onchial complex, slightly from side, showing separation of mandibular rods and mandibular plate. Fig. 69. *En face* view of head with lip-lobes folded posteriorly over lips. Fig. 70. Longitudinal section of lip showing distribution of Muscle-1 and posterior extension of onchial cavity (pocketed condition : see page 279). Fig. 71. Lateral view of male tail. Fig. 72. Dorsal lip from outer surface showing distribution of nerves to labial sense organs relative to cephalic ring and mandibular complex. Fig. 73. Detail of spicules and gubernaculum. Note the barbed posterior end to spicule.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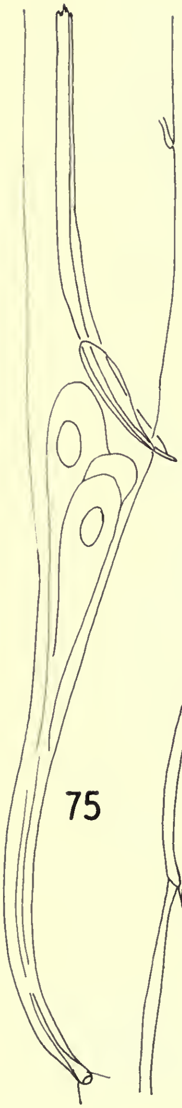
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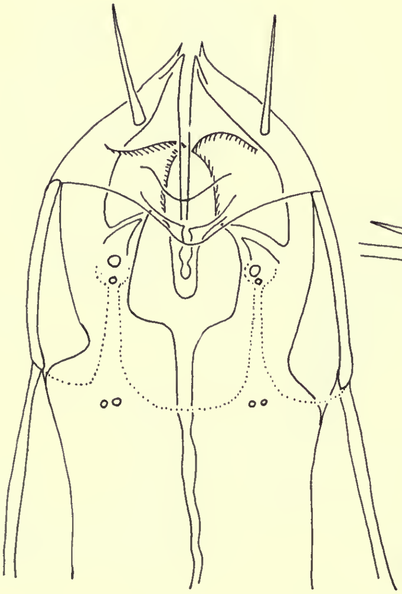
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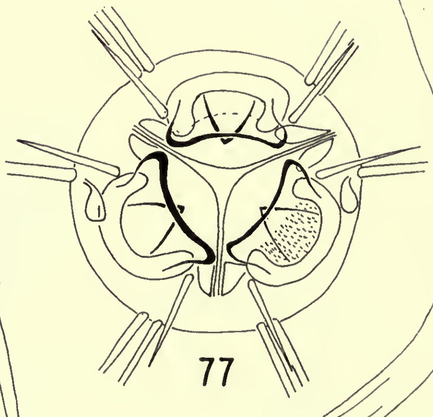
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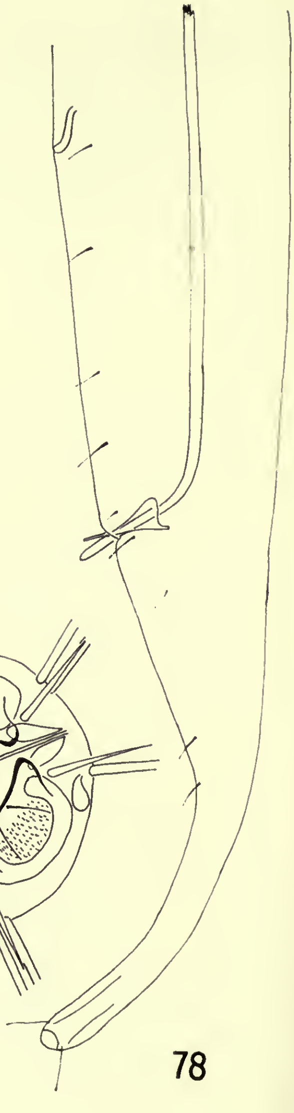
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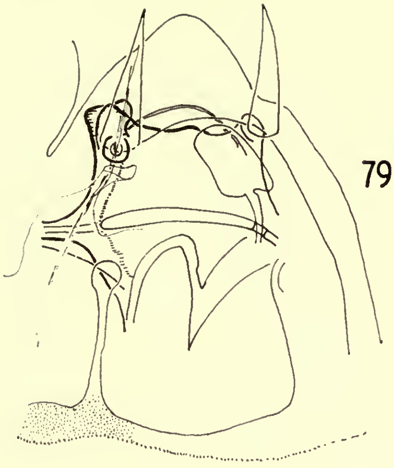
FIGS. 74 and 75. *Mescanthion ceeus*. Fig. 74. Dorsal lip from outer surface. Fig. 75. Lateral view of male tail (spicule not shown completely because of its length).
FIGS. 76–78. *M. cavei*. Ventral view of head. Fig. 77. Simplified *en face* view of head. Fig. 78. Lateral view of male tail (spicule not shown completely).



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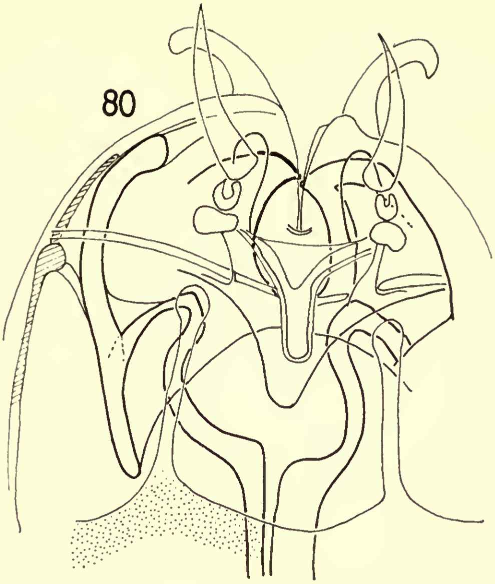

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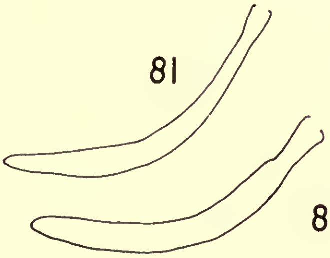

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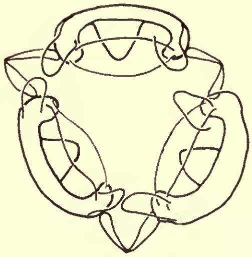

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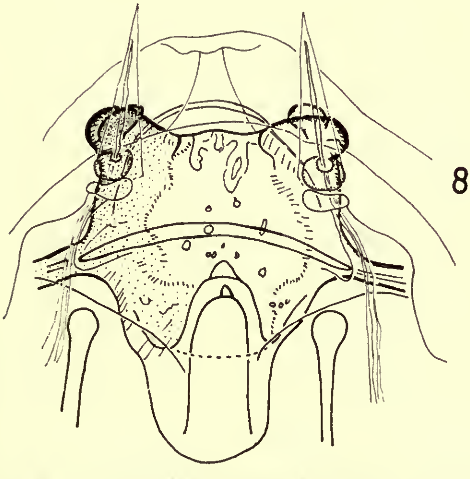

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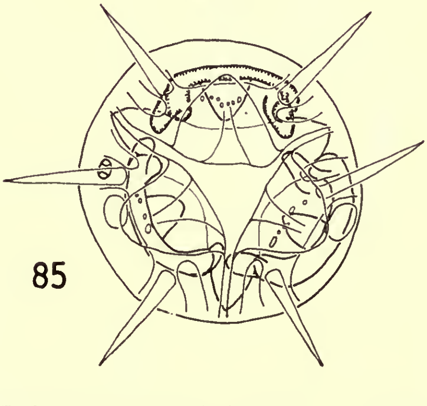

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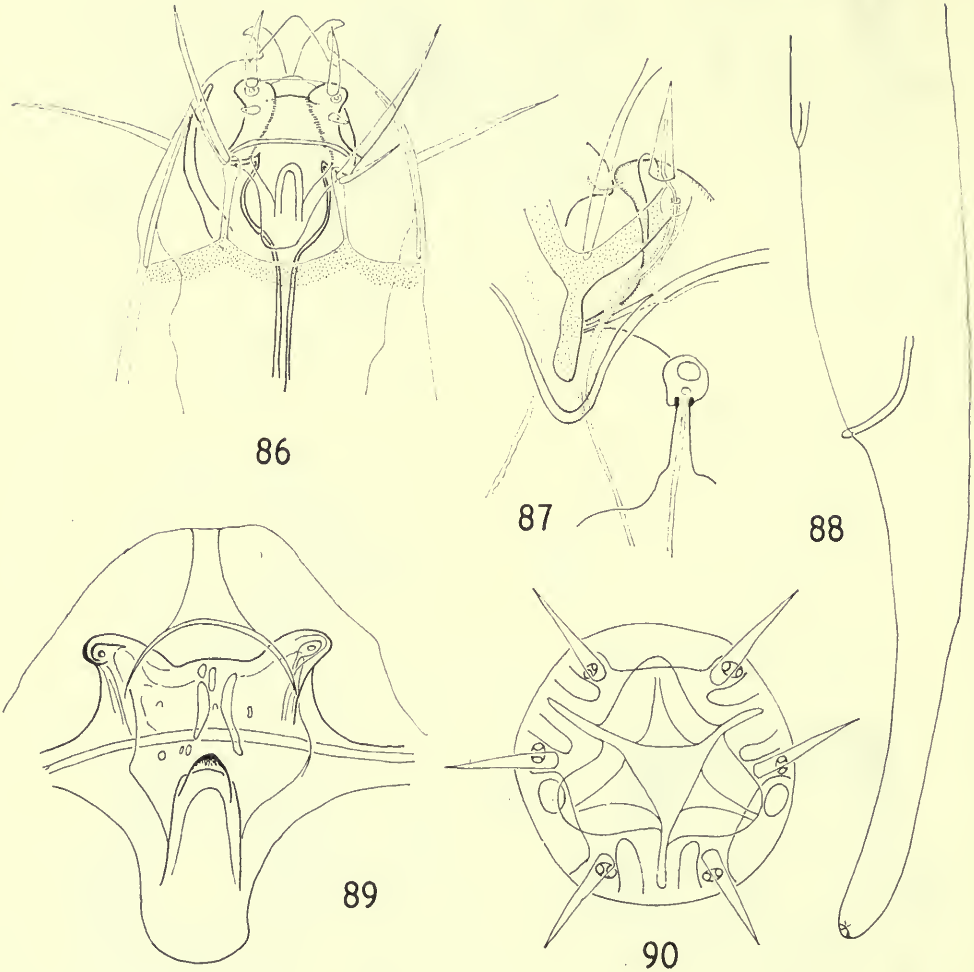
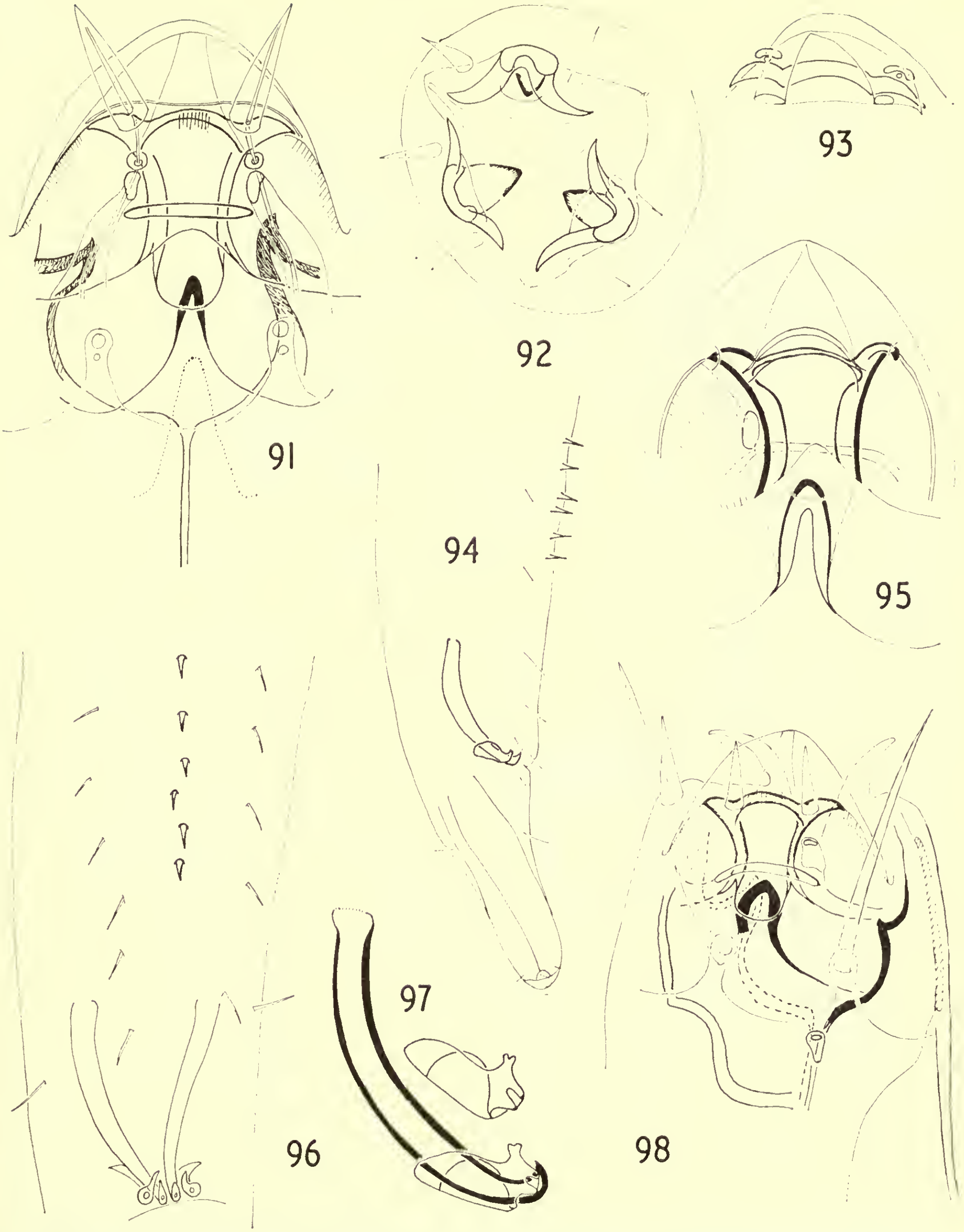
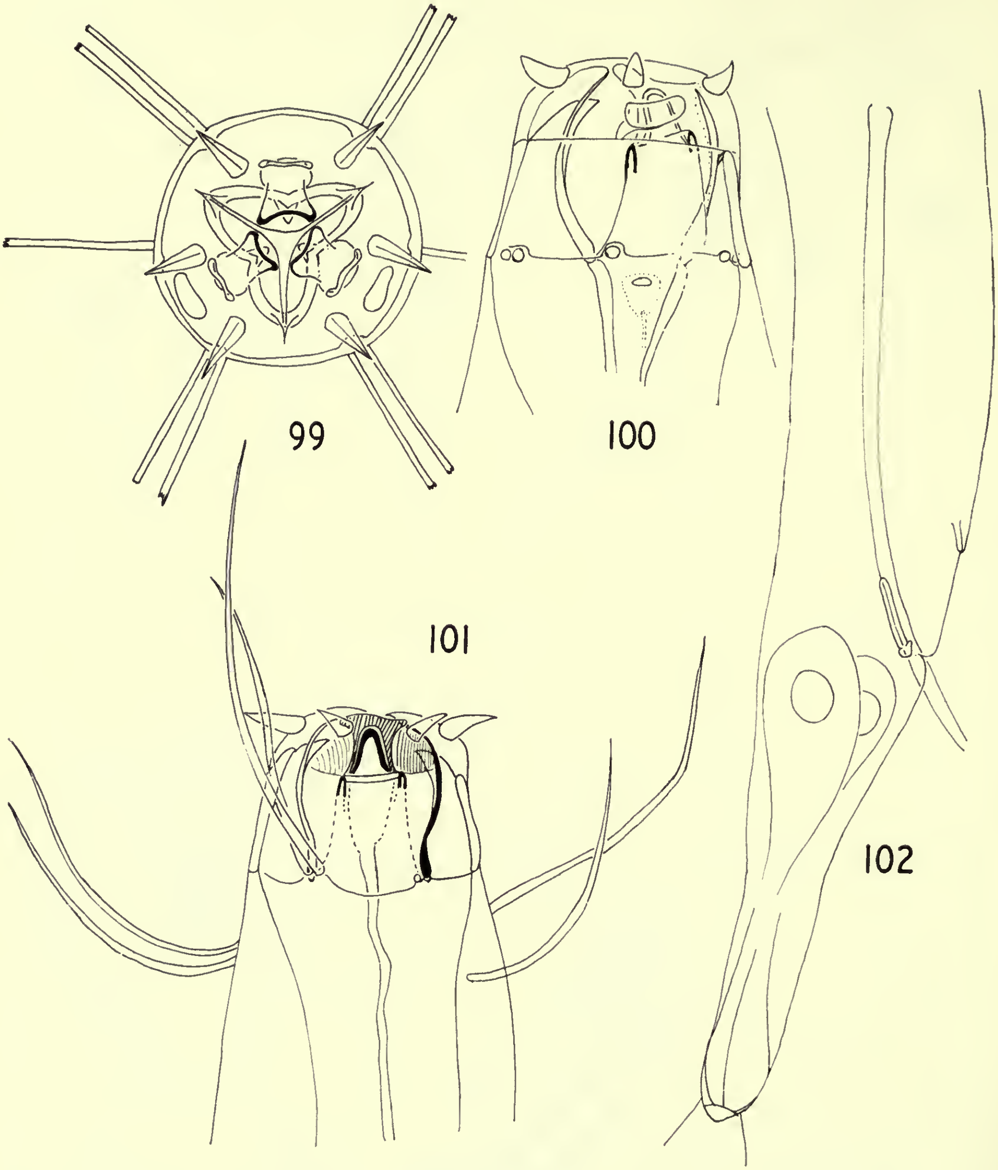
Figs. 79–85. *Mesacanthion studiosa.* Fig. 79. Left ventro-lateral lip from the outer surface showing large pocket of cephalic slit and distribution of nerve to labial sense organ. Fig. 80. Ventral view of head showing cephalic capsule and mandibular : onchial complex in optical section. Figs. 81 and 82. Representative spicules. Fig. 83. *En face* view of mandibular : onchial complex. Fig. 84. Detail of dorsal lip from outer surface showing distribution of nerves to labial sense organs, cephalic ring, almost wholly absorbed mandibular rods and massive fusion of mandibular and onchial components of skeletal system. Fig. 85. *En face* view of head.



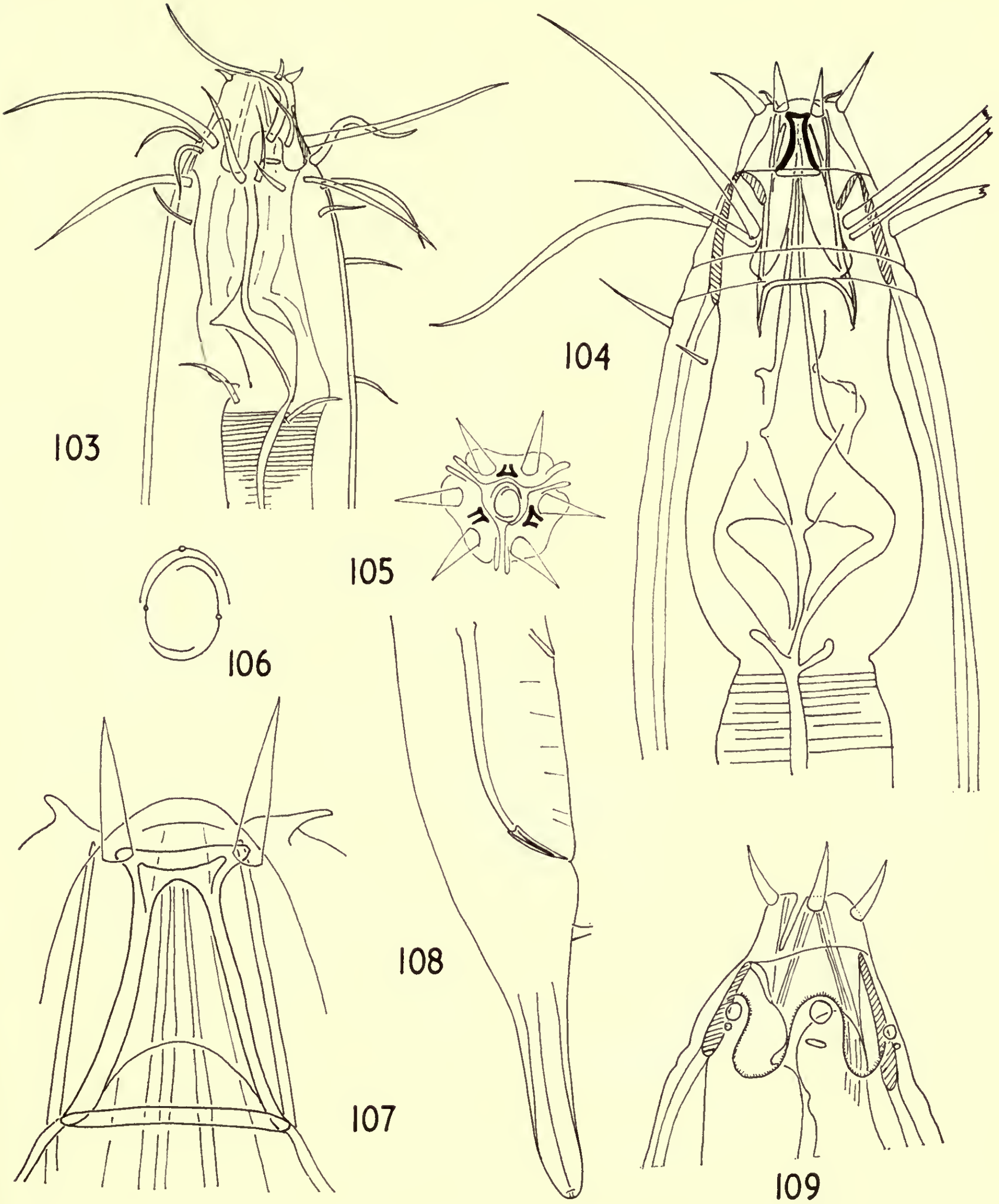
Figs. 86–90. *Mescanthion studiosa*. Fig. 86. General dorsal view of head. Fig. 87. View taken at end of a radius showing distribution of nerve to labial sense organ and its relationship to cephalic ring. Fig. 88. Lateral view of male tail. Fig. 89. View of lip from inner surface. Fig. 90. *En face* view of head showing anterior modifications of cephalic capsule.



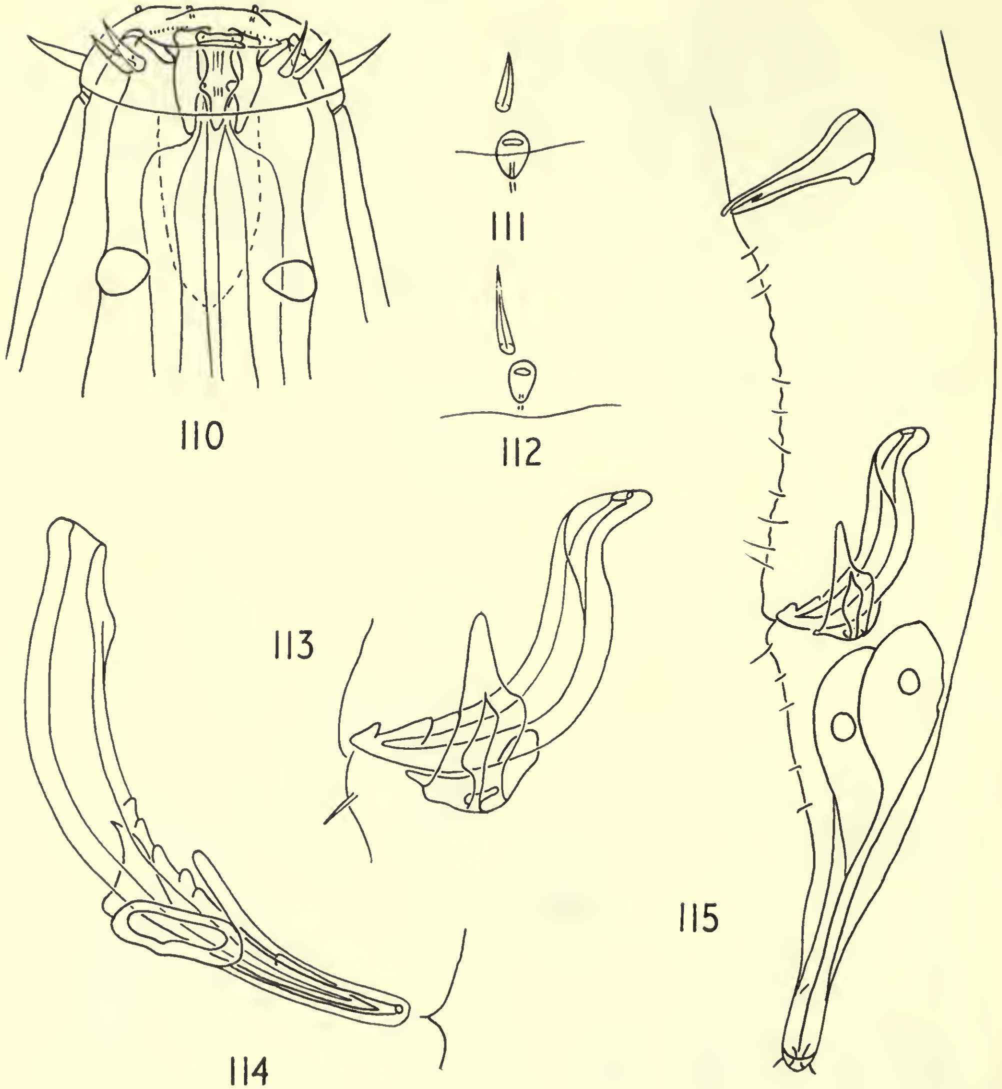
Figs. 91–98. *Africanthion nudus.* Fig. 91. Dorsal lip from outer surface. Fig. 92. *En face* view of head. Fig. 93. *En face* detail of mandible showing thickenings of edges of labial lobes. Fig. 94. Lateral view of male tail. Fig. 95. Left ventro-lateral lip from the inner surface. Fig. 96. Ventral view of male body anterior to cloacal opening showing distribution of pre-cloacal setae. Fig. 97. Detail of spicules and gubernaculum from the lateral aspect. Fig. 98. Left ventro-lateral lip from the outer surface showing small amphid and cephalic slit.



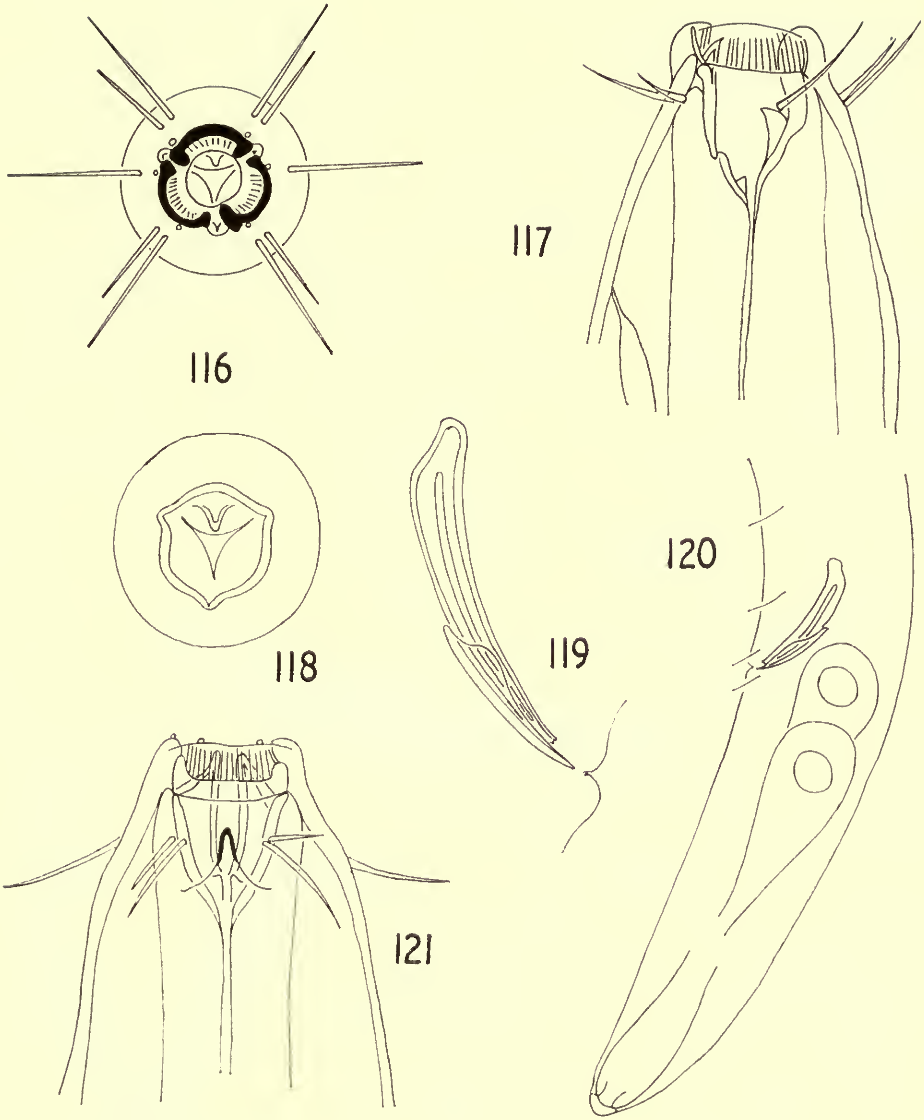
FIGS. 99–102. *Trileptium ayum*. Fig. 99. *En face* view of head. Fig. 100. Lateral view of head with the dorsal surface to the left. Fig. 101. Dorsal view of head. Note particularly the way in which the onchium is closely embraced by the mandible. Fig. 102. Lateral view of male tail.



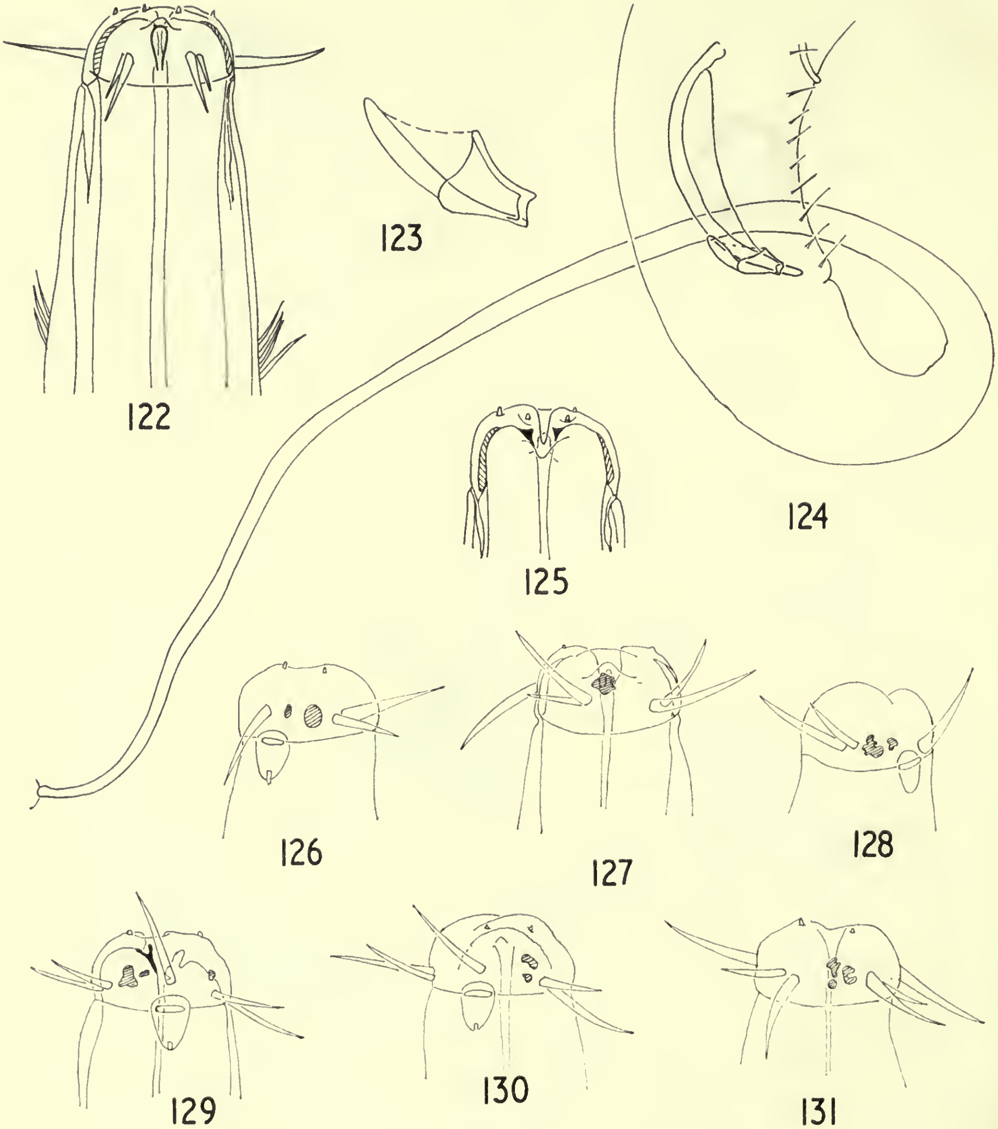
Figs. 103–109. *Thoracostomopsis carolae.* Fig. 103. General view of male head from the lateral aspect. Fig. 104. Dorsal view of female head. Fig. 105. *En face* view of head. Fig. 106. Diagram of *en face* appearance of plate-like onchia. Fig. 107. Free-hand sketch of anterior, mandibular, part of dorsal lip. Fig. 108. Lateral view of male tail. Fig. 109. Detail of cephalic capsule from the lateral aspect.



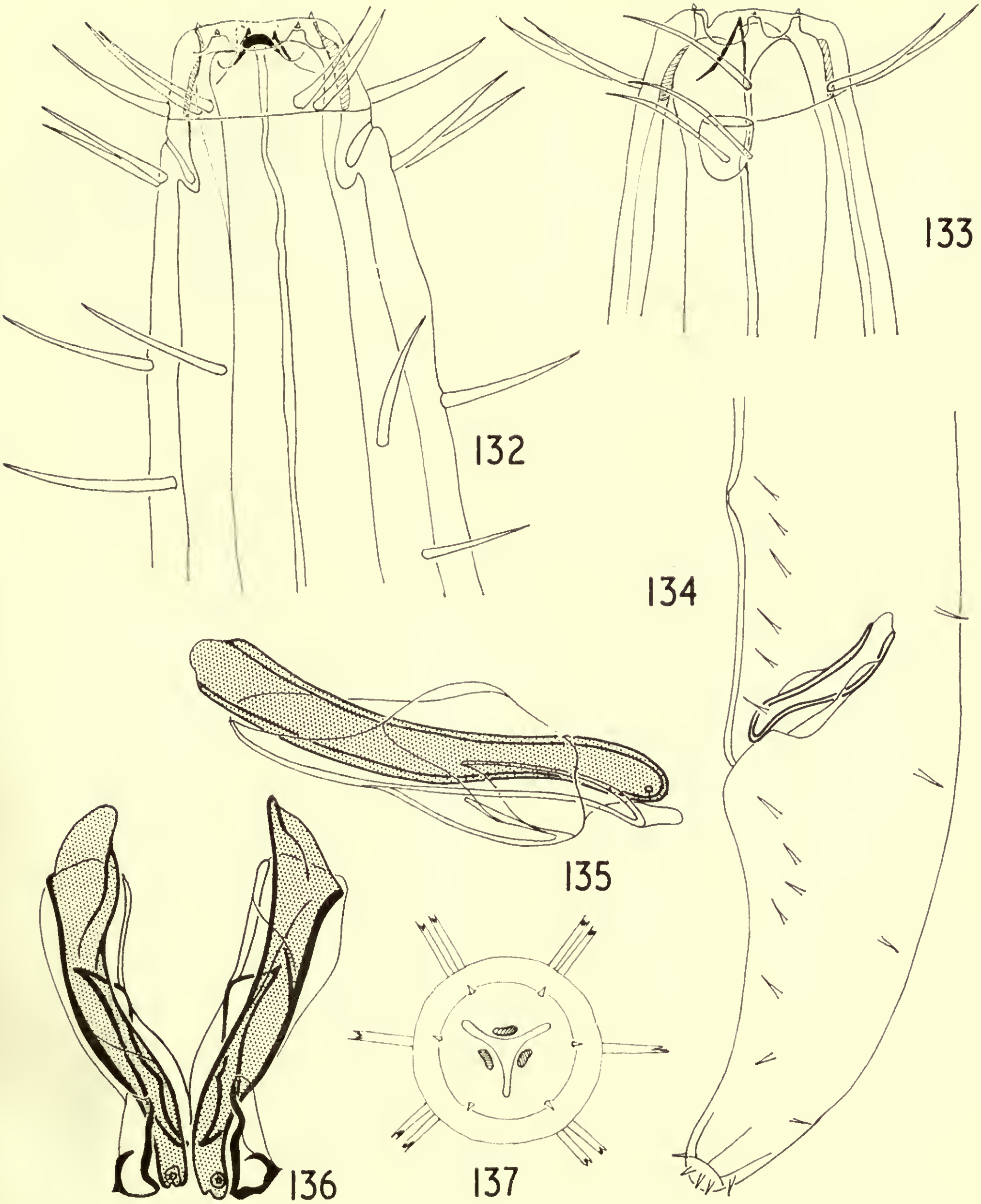
Figs. 110–115. *Enoplus.* Fig. 110. *E. harlockae.* Dorsal view of head. Fig. 111. *E. harlockae.* Relationship of amphid to posterior edge of cephalic capsule. Fig. 112. *E. michaelseni.* Relationship of amphid to posterior edge of cephalic capsule. Fig. 113. *E. harlockae.* Detail of spicules and gubernaculum. Fig. 114. *E. michaelseni.* Detail of spicules and gubernaculum. Fig. 115. *E. harlockae.* Lateral view of male tail.



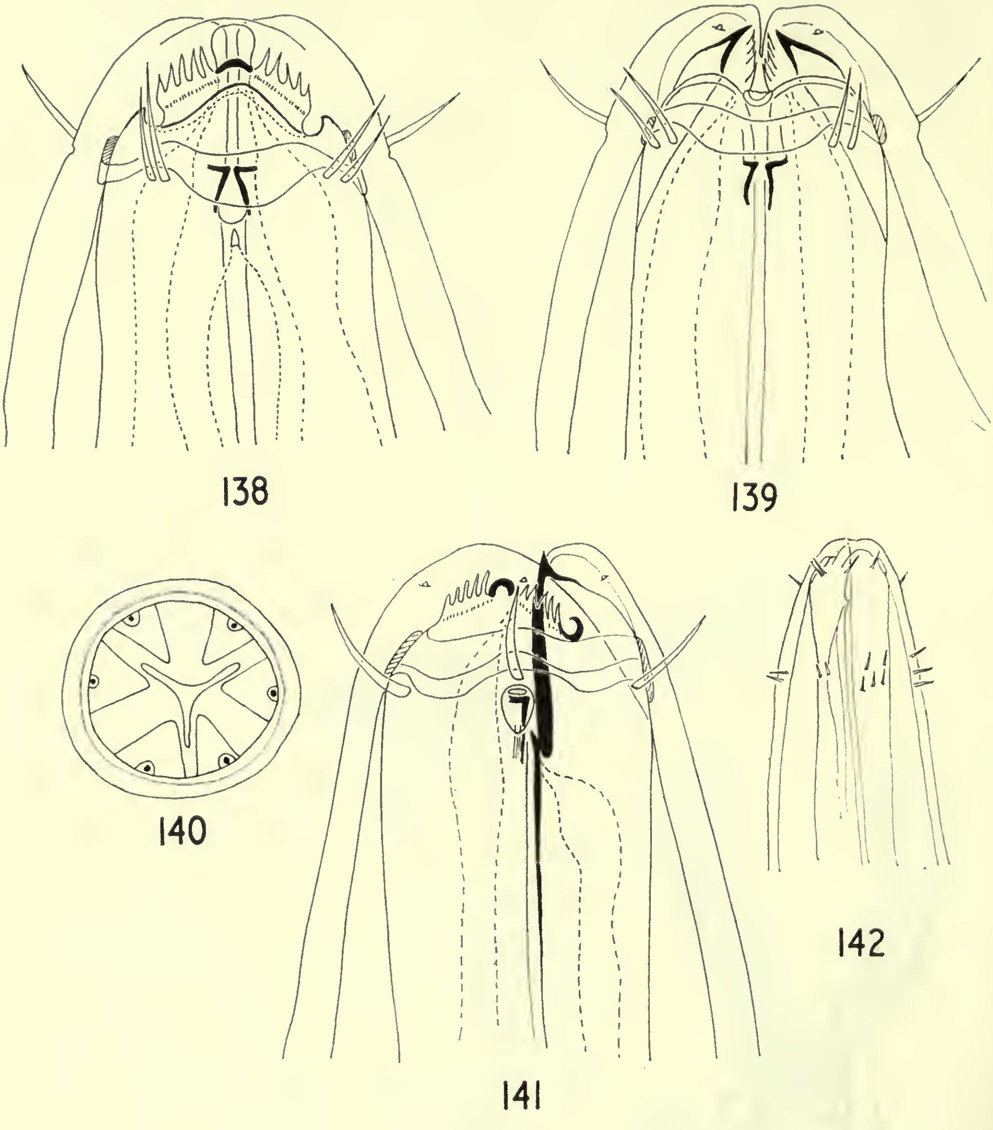
Figs. 116–121. *Rhabdodemania nancyae*. Fig. 116. *En face* view of head. Fig. 117. Lateral view of head with the dorsal surface to the right. Fig. 118. *En face* optical section through onchial cavity showing large dorsal onchium. Fig. 119. Detail of spicules and gubernaculum. Fig. 120. Lateral view of male tail. Fig. 121. Dorsal view of head.



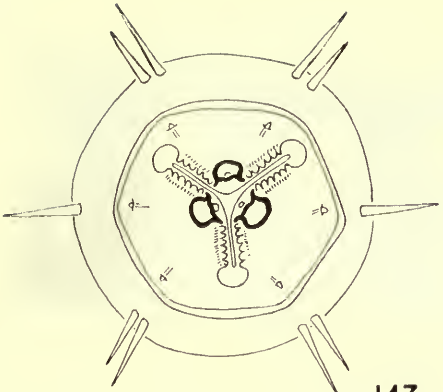
Figs. 122–131. *Anticoma chitwoodi*. Fig. 122. Dorsal view of head. Fig. 123. Detail of gubernaculum. Fig. 124. Lateral view of male tail. Fig. 125. Ventral view of head. Figs. 126–131. Views of head showing lacunae in cephalic capsule. Fig. 126, left dorso-lateral ; Fig. 127, dorsal ; Fig. 128, right dorso-lateral ; Fig. 129, left lateral ; Fig. 130, right ventro-lateral ; Fig. 131, ventral.



Figs. 132–137. *Parabarbonema barba.* Fig. 132. Dorsal view of anterior end of body. Fig. 133. Lateral view of head with the dorsal surface to the left. Fig. 134. Lateral view of male tail. Fig. 135. Detail of spicules and gubernaculum from the lateral aspect. The spicule is stippled. Fig. 136. Ventral view of spicules and gubernaculum. The spicules are stippled. Fig. 137. *En face* view of head.



FIGS. 138–142. *Macronchus shealsi*. Fig. 138. Dorsal view of head. Fig. 139. Ventral view of head. Fig. 140. Deep *en face* view of head. Fig. 141. Lateral view of head. Fig. 142. Lateral view of anterior end of body.



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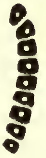

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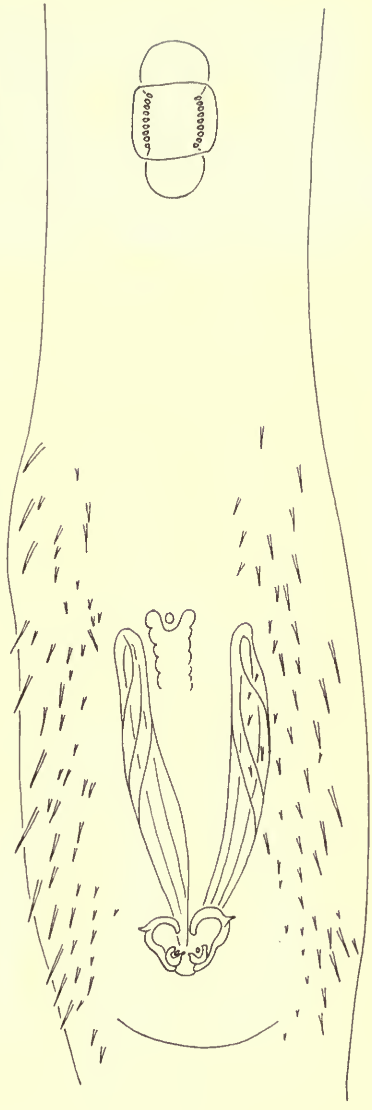

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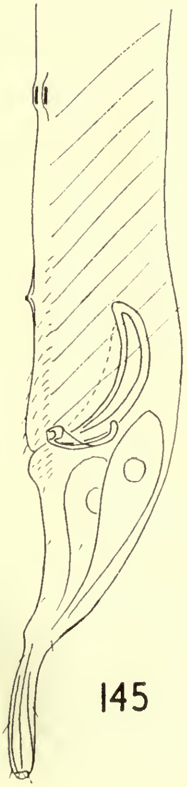

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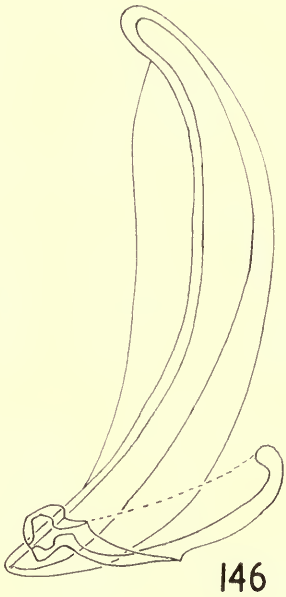

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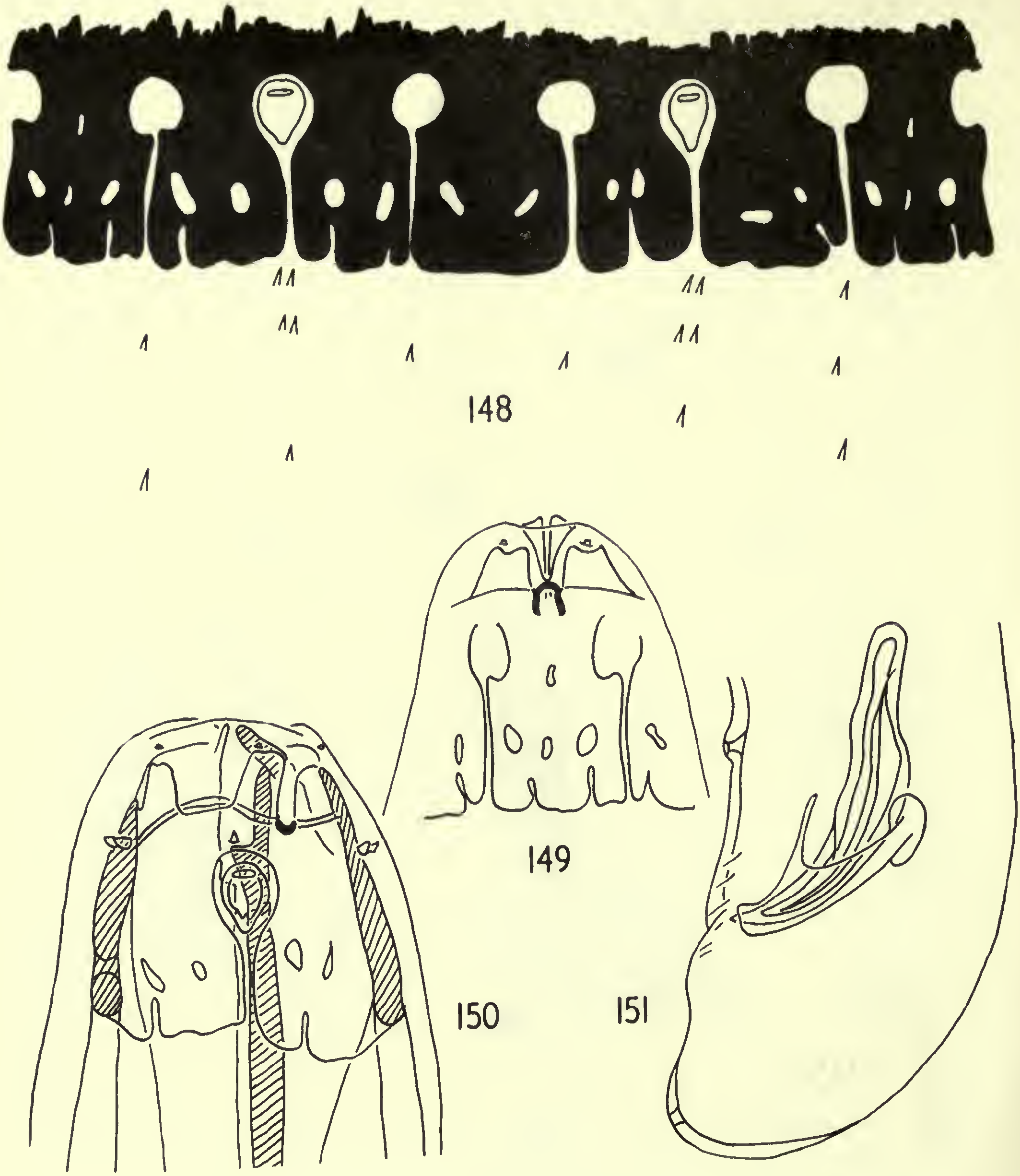
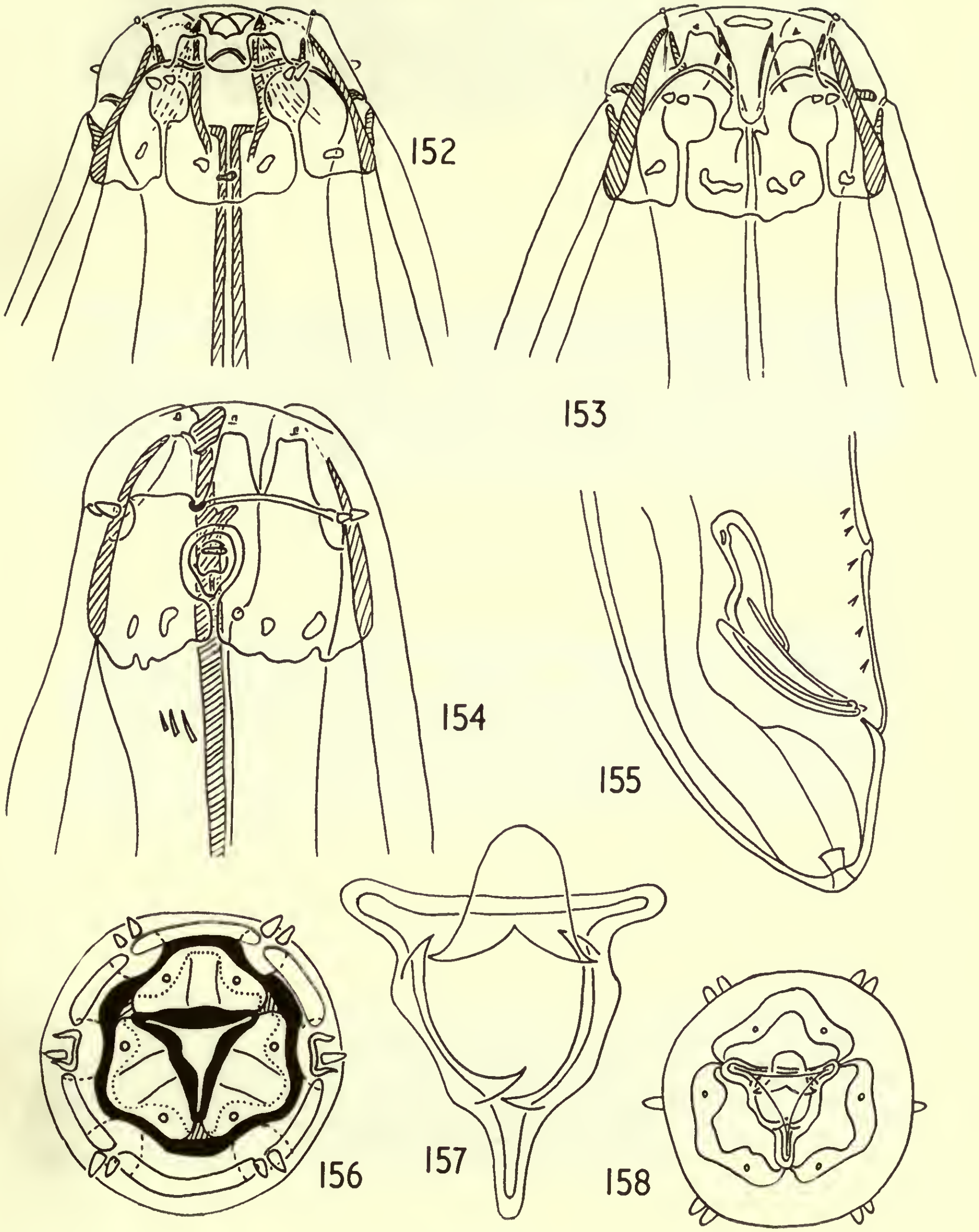
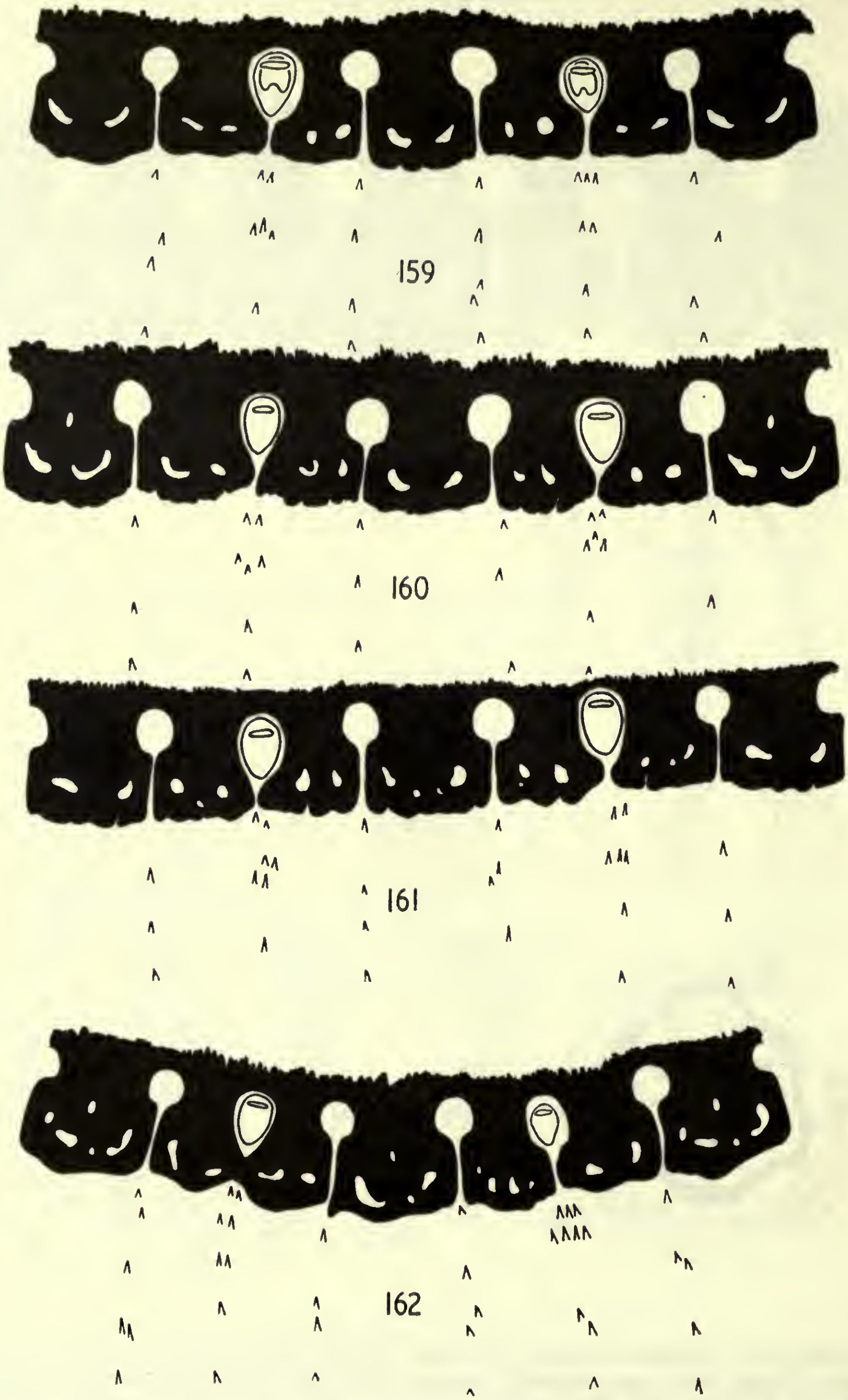
FIGS. 143–147. *Macronchus shealsi*. Fig. 143. *En face* view of head. Fig. 144. Detail of cuticular structure, of one side, in anterior pre-cloacal supplement. Fig. 145. Lateral view of male tail. Fig. 146. Detail of spicules and gubernaculum. Fig. 147. Ventral view of male body anterior to cloacal opening showing distribution of setae and the disposition and appearance of the pre-cloacal supplements. Note the form of the posterior ends of the gubernaculum.



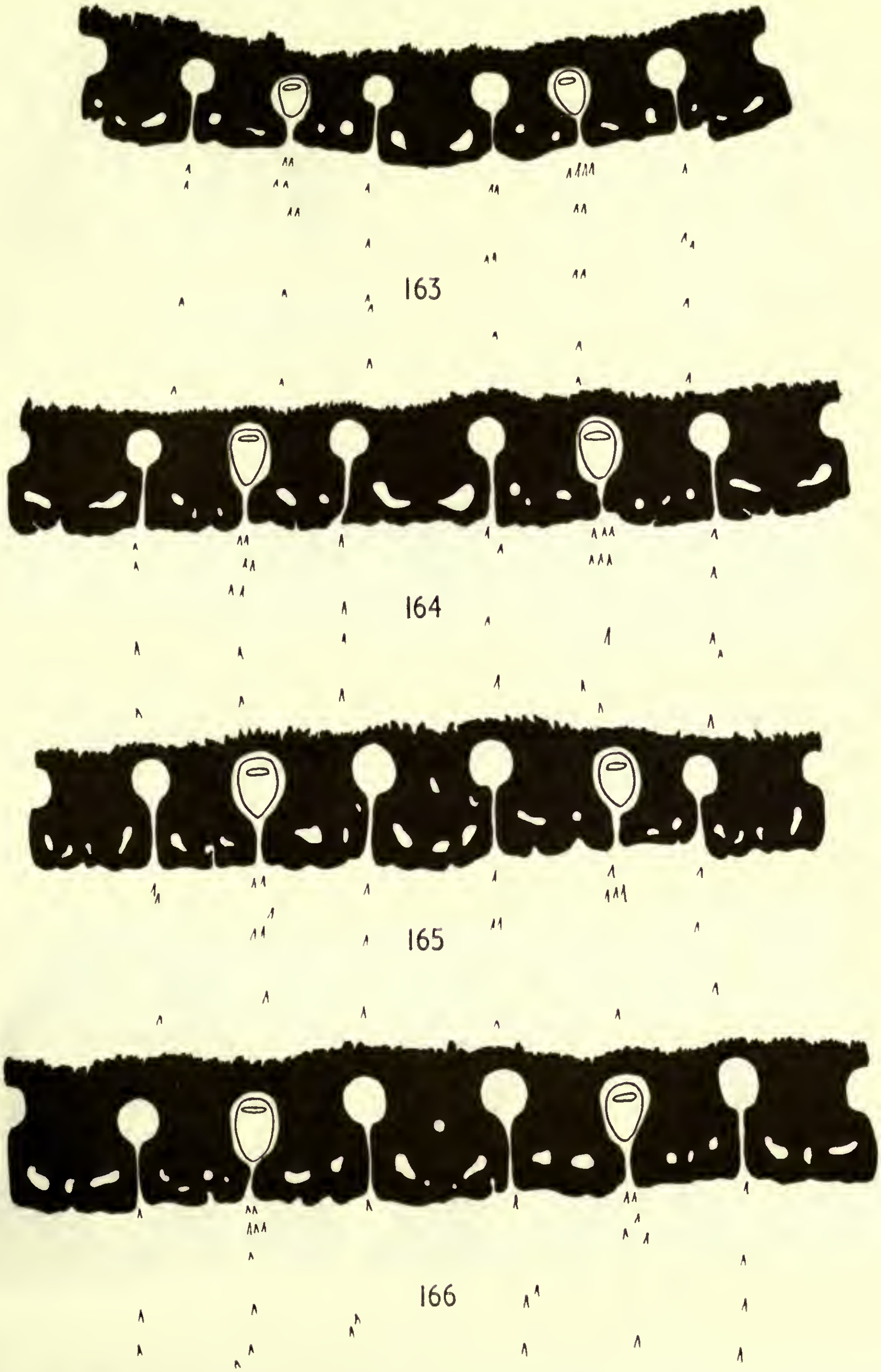
Figs. 148–151. *Thoracostoma angustifissulatum.* Fig. 148. Posterior part of the cephalic capsule with the ventral lobe at each end and the dorsal lobe in the centre. Anterior edge not in detail. Fig. 149. Ventral view of head. Fig. 150. Lateral view of head with the dorsal surface to the right. Fig. 151. Lateral view of male tail.



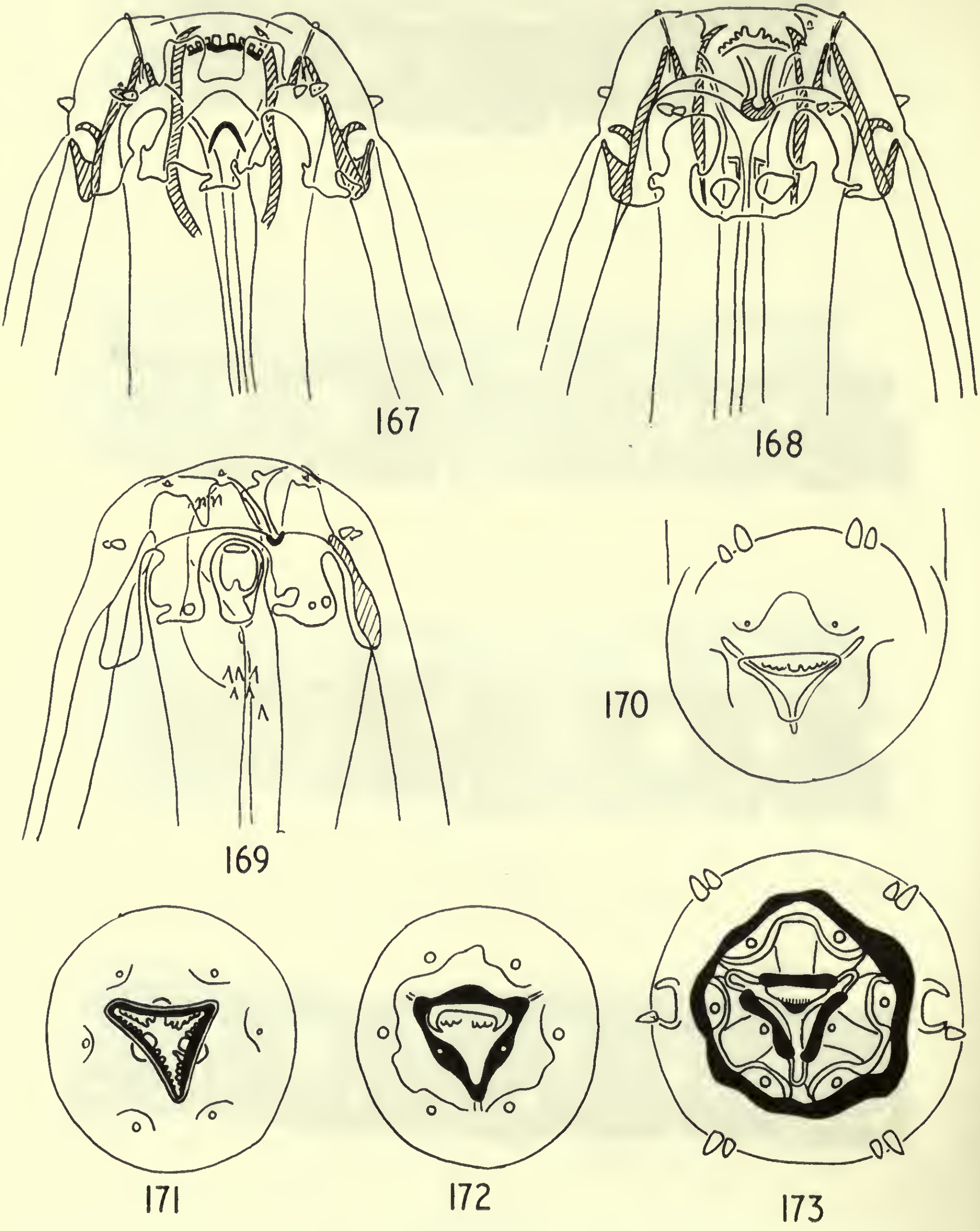
Figs. 152–158. *Thoracostoma jae.* Fig. 152. Dorsal view of head. Fig. 153. Ventral view of head. Fig. 154. Lateral view of head with the dorsal surface to the left. Fig. 155. Lateral view of male tail. Fig. 156. Deep *en face* view of head. Fig. 157. Sketch of buccal armature. Fig. 158. *En face* view of head, superficial.



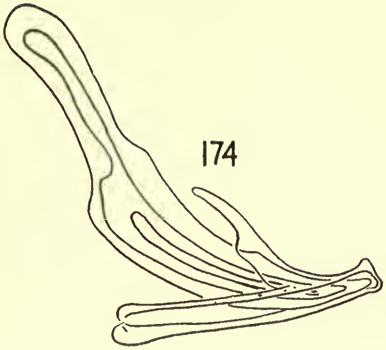
Figs. 159–162. *Thoracostoma jae.* Detail of posterior edge of cephalic capsule and distribution of nuchal setae with ventral lobe at each side and dorsal lobe in centre. Anterior edge not in detail. All males. Fig. 159. 8·3 mm. body length. Fig. 160. 8·8 mm. Fig. 161. 7·2 mm. Fig. 162. 7·6 mm.



Figs. 163–166. *Thoracostoma jae*. Detail of posterior edge of cephalic capsule. Anterior edge not in detail. Fig. 163. Larva of 6·9 mm. body length. Fig. 164. Female, 8·4 mm. Fig. 165. Female, 7·4 mm. Fig. 166. Female, 9·0 mm.



FIGS. 167–173. *Thoracostoma zeae*. Fig. 167. Dorsal view of head. Fig. 168. Ventral view of head. Fig. 169. Lateral view of head with dorsal surface to the right. Fig. 170. Oblique dorsal view of mouth opening. Fig. 171. *En face* view of head, surface. Fig. 172. The same, slightly below surface. Fig. 173. The same, deep.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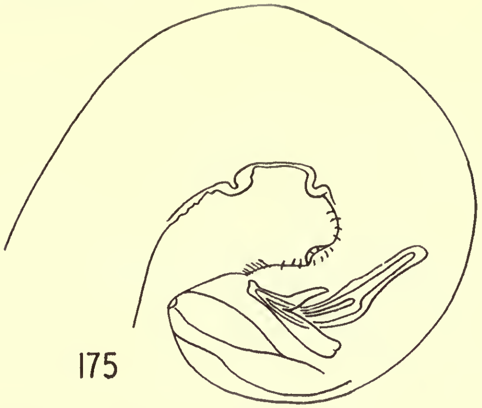
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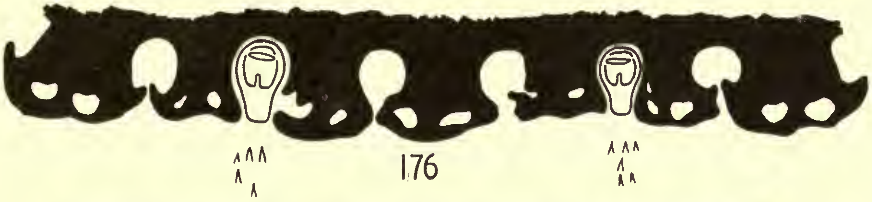
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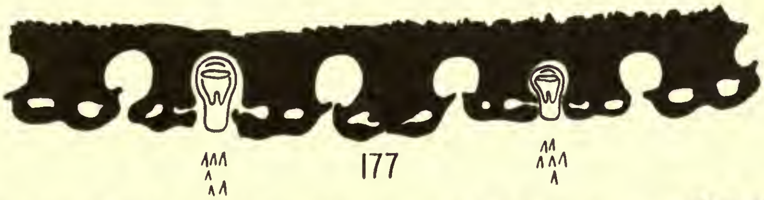
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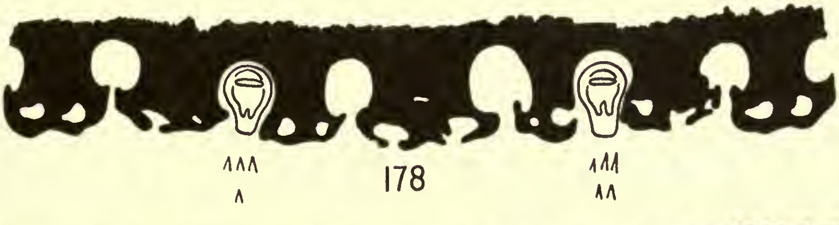
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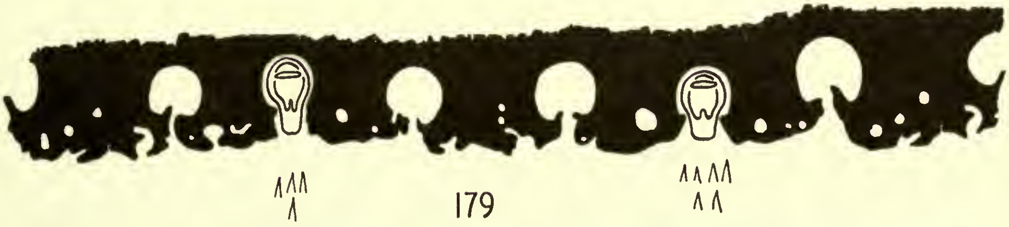
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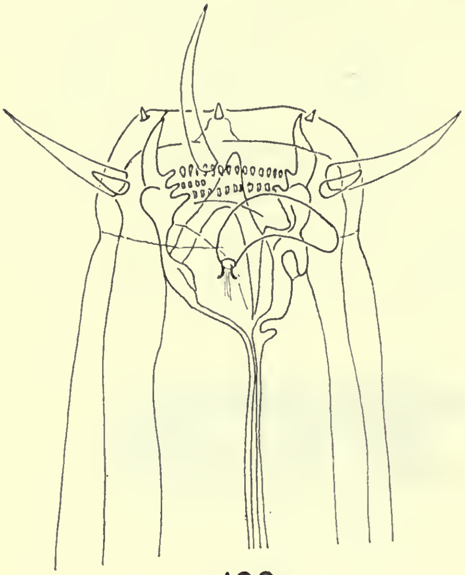
FIGS. 174–179. *Thoracostoma zeae*. Fig. 174. Detail of spicules and gubernaculum. Fig. 175. Lateral view of male tail. Figs. 176–179. Posterior part of the cephalic capsule with the ventral lobe at each side and the dorsal lobe in the centre. Anterior edge not in detail. Figs. 176–178. Larvae. Fig. 179. Male.



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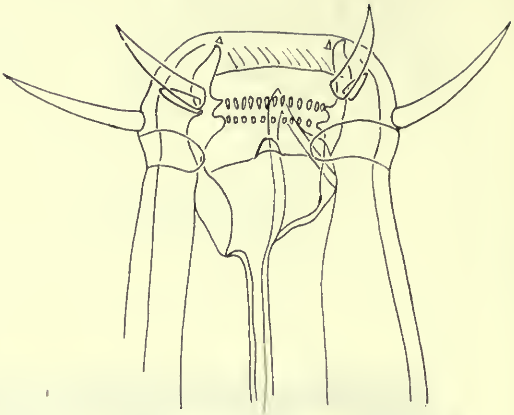

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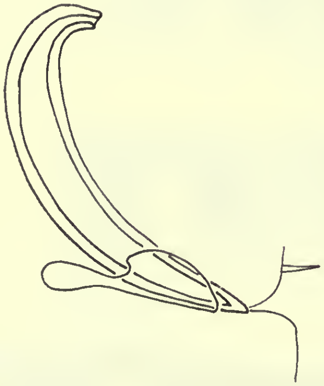

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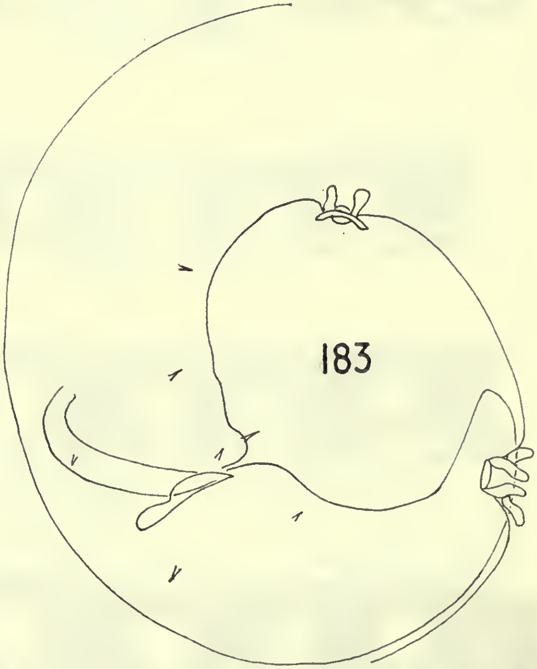

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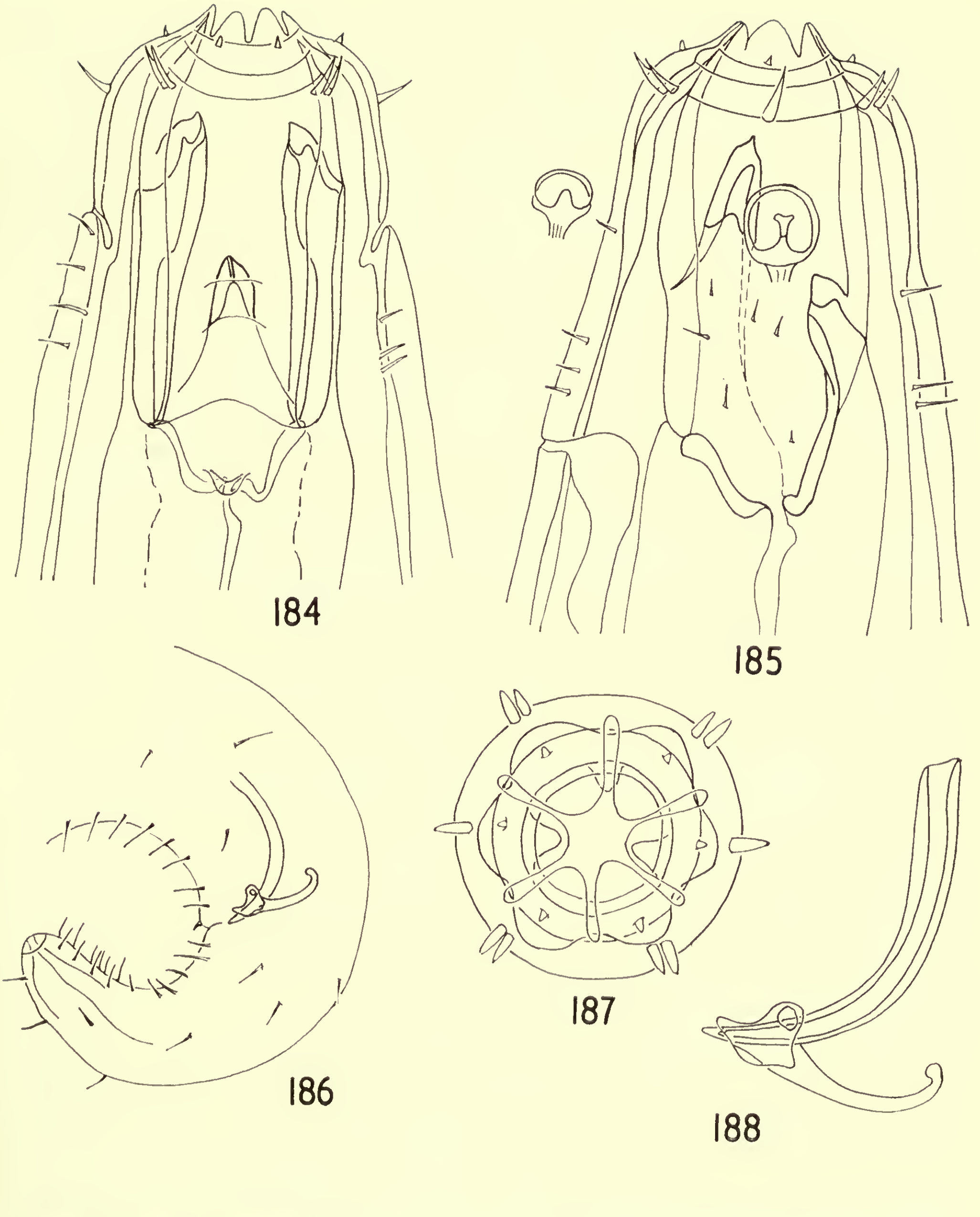
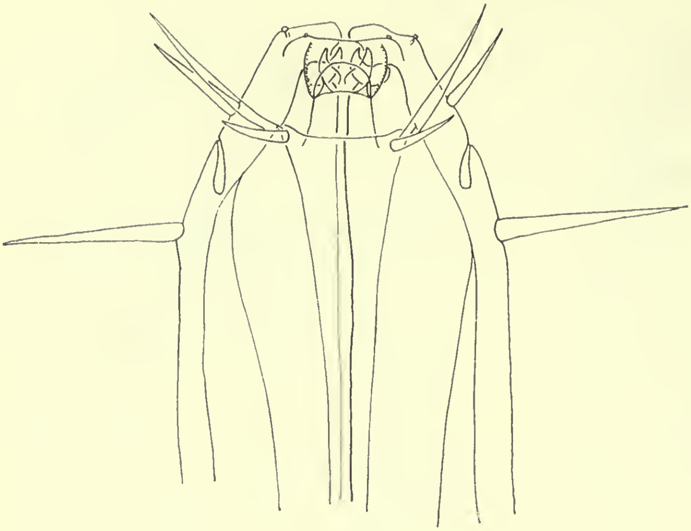
FIGS. 180–183. *Eurystomina sudensis*. Fig. 180. Lateral view of head with the dorsal surface to the right. Fig. 181. Dorsal view of head. Fig. 182. Detail of spicules and gubernaculum. Fig. 183. Lateral view of male tail.



FIGS. 184–188. *Pontonema yaena*. Fig. 184. Dorsal view of head. Fig. 185. Lateral view of head with the dorsal surface to the right. Variant amphid form shown to the left. Fig. 186. Lateral view of male tail. Fig. 187. *En face* view of head. Fig. 188. Detail of spicules and gubernaculum.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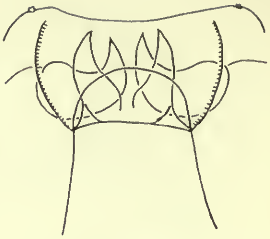
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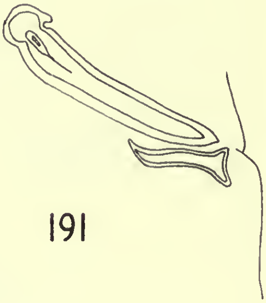
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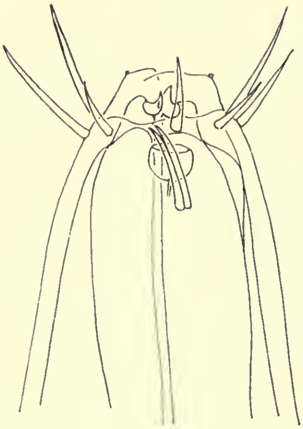
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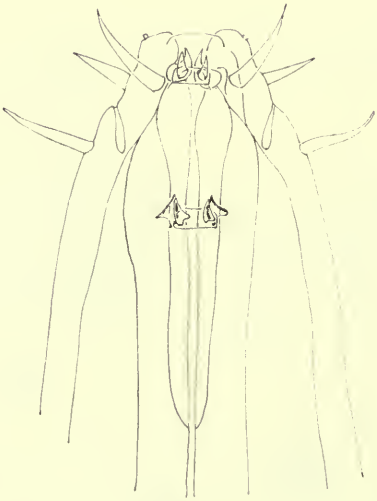
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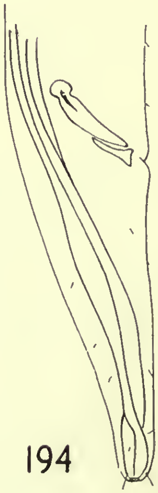
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Figs. 189–194. *Thalassironus jungi.* Fig. 189. Dorsal view of head. Fig. 190. Detail of buccal dentition. Fig. 191. Detail of spicules and gubernaculum. Fig. 192. Lateral view of anterior end. Fig. 193. Dorsal view of larval head. Fig. 194. Lateral view of male tail.

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THE SWIMBLADDER IN AFRICAN NOTOPTERIDAE (PISCES) AND ITS BEARING ON THE TAXONOMY OF THE FAMILY

P. H. GREENWOOD

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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BY

P. H GREENWOOD
Department of Zoology, British Museum (Natural History)

Pp. 377–412 ; *Plates* 1–4 ; 5 *Text-figures*

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By P. H. GREENWOOD

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INTRODUCTION

THE swimbladder in Asian Notopteridae has long been the subject of discussion and investigation (Cuvier and Valenciennes, 1848 ; Bridge, 1900 ; de Beaufort, 1909 ; Dehadrai, 1957 & 1962 ; Marshall, 1962) but the African representatives (*Notopterus afer* and *Xenomystus nigri*) have never been studied ; authors have tacitly assumed uniformity in this organ throughout the family. Marshall (1962) has recently suggested the importance of swimbladder studies in understanding the higher classification of isospondylous fishes. He also drew attention to the still unsettled taxonomic position of the North American Hiodontidae in relation to the Notopteridae.

In this paper I have attempted both to fill the gap in our knowledge of notopterid swimbladders and to review the phyletic position of the Hiodontidae. A preliminary note on the first aspect of this problem has already appeared (Greenwood, 1963). From the investigations it is clear that the African notopterids differ significantly from their Asian congeners and that these differences must affect the current taxonomy of the family. So, in addition to the anatomical descriptions a short taxonomic section is appended, together with a discussion on the broader taxonomic implications arising from these investigations.

THE SWIMBLADDER OF *NOTOPTERUS AFER**

(i) *Abdominal Part* (Plates 1–4 and Text-fig. 1)

As in the Asian species, the swimbladder is divisible into a cranial (precoelomic), an abdominal and a caudal (post-coelomic) part.

Two subdivisions of the *abdominal* part are easily recognized from external features ; there is an anterior, subspherical portion with thick, fibrous and silver-grey walls from which is derived a wedge-shaped posterior projection (most easily discerned on the left side) overlying the second division, a thin walled, muscle

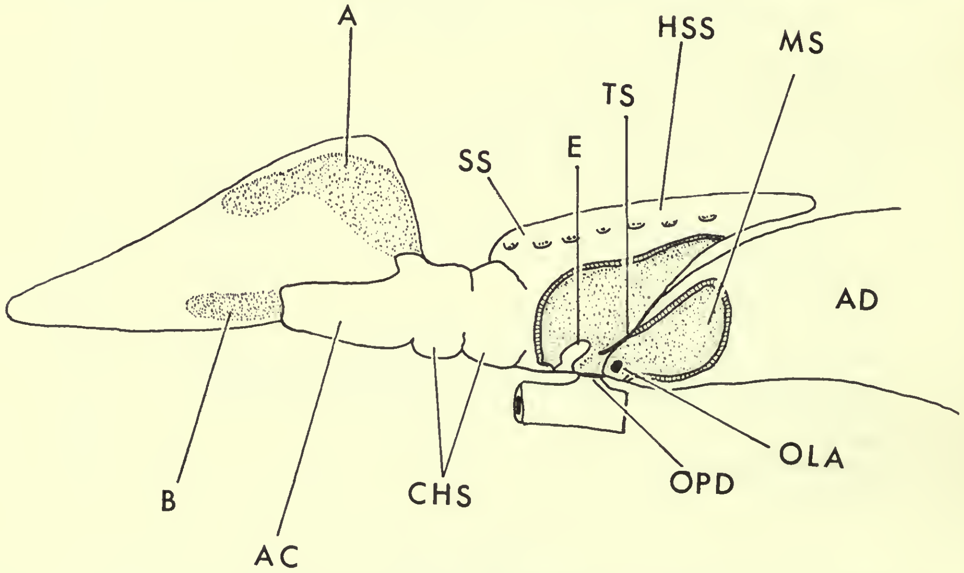

FIG. 1. *Notopterus afer*. Diagrammatic representation of the cephalic and abdominal portions of the swimbladder ; left lateral view. Part of the lateral wall is removed from the subspherical sac and the anterior portion of the abdominal section. The crescentic markings on the subspherical sac and its posterior horn represent the points through which the ribs emerge. The neurocranium is indicated diagrammatically in outline. A : superior intracranial diverticulum ; AC : auditory chamber ; AD : abdominal division of swimbladder ; B : inferior intracranial diverticulum ; CHS : contiguous hemispheres ; E : epiglottis ; HSS : posterior horn of subspherical sac ; MS : median septum dividing anterior (fused) portion of abdominal swimbladder ; OLA : opening to left-hand division of abdominal swimbladder ; OPD : opening of pneumatic duct ; SS : subspherical sac ; TS : oblique transverse septum dividing abdominal and subspherical divisions of the swimbladder.

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*Later, this species is placed in a new genus, but throughout the anatomical section it will be referred to by its better known name.

invested, elongate sac (Plates 1 & 2 ; Text-fig. 1). These superficial divisions coincide with internal structural differences which are described below. The large pneumatic duct enters the swimbladder through the base of the subspherical sac near its posterior limits. On first dissection, the division between the subspherical sac and the posterior sac is obscured by a large, descending lobe of kidney. At about the ventral margin of the swimbladder, this kidney lobe sends back a thinner, horizontal lobe which is closely applied to the ventral wall of the bladder over its entire abdominal extent.

The subspherical sac is large, and from it is developed the wedge-shaped projection noted above (Text-fig. 1). Internally, the wedge is divided medially by the vertebral column. Each horn so formed must be considered as a separate diverticulum. The external tunic of the subspherical sac and its horns is very tough and fibrous, having the appearance and feel of leather. Dorsally it is inserted onto the dorsolateral surface of the vertebral column, just above the ribs. The proximal parts of the first seven ribs are thus covered by the *tunica externa.* At the point where each rib curves ventrad it penetrates the tunic and thus comes to lie outside the bladder, closely embracing its lateral wall. The proximal sixth of each rib, after it has left the bladder, is encased in a gutter-like sleeve of *tunica externa* which leaves the dorsal aspect of the rib uncovered ; laterally and ventrally, the tunic sleeve is closely applied to the rib. Within the bladder, each rib is closely covered on its anterior, ventral and posterior face by the thin *tunica interna.*

The subspherical sac is connected to the cranial chamber by means of two, shorter, contiguous, somewhat flattened hemispherical sacs lying above the posterior part of the branchial chamber (Text-fig. 1). The more posterior of these sacs is linked to the subspherical sac through an elongate " waist ", lying between the cleithra. Like the abdominally situated subspherical sac, these anterior chambers have a thick, fibrous external tunic. Although not strictly cranial in position, this portion of the bladder will be described with the cranial section.

Internally, the anterior limit of the subspherical sac is recognizable by a low ridge, developed from the *tunica externa,* and appearing as two half rings rising vertically from a median ridge in the floor of the sac (Plate 3). Each half ring runs vertically up the wall of the sac and ends at the vertebral column. A number of similar rings strengthen the walls of the posterior horns arising from the sac. Since the *tunica externa* ends at its insertion on the vertebral column, the roof of the subspherical sac, and the median walls of the two horns, are formed entirely from the very thin *tunica interna.* In preserved specimens this tunic is transparent and since it is intimately applied to the vertebrae, the details of these bones are easily seen (Plate 4).

Anteriorly the lumen of the subspherical sac is continuous with that of the interconnecting and cranial chambers. Posteriorly, however, it is sealed off from the thin-walled abdominal sac by an almost complete, gently curved and oblique transverse wall. The only perforation in this wall is situated ventrally (see below, p. 382 and Plate 3).

Besides forming a transverse partition, the wall also forms the floor to the posterior horns of the subspherical sac. It will be recalled that these horns are actually a single, wedge-shaped chamber arising from the subspherical sac and overlie the anterior part of the thin-walled sac ; internally the chamber is divided into two by the vertebral column. The relationship of the horns with the underlying chamber of the abdominal bladder differs in the large and smaller specimens examined. In the two large specimens (48·0 & 53·5 cm. S.L., both females), the wall forms a common boundary between the right horn and the right hand side of the abdominal sac (which is divided into left and right chambers anteriorly by a median vertical septum, see below) ; in the smallest fish (30 cm. S.L. ; possibly a male) there is a common boundary between the horn and the sac on both sides. By contrast, in the large fishes, the left horn is distinct from the underlying abdominal sac, so the continuation of the oblique transverse wall merely forms a floor to the horn (see Plate 3), the sac having its own dorsal wall. Where there is a common boundary between horn and sac (right side in large fishes, both sides in the smaller individual) it is perforated and the two cavities are in communication ; also in these cases, the *tunica externa* of the two divisions is continuous laterally so that externally it is impossible to distinguish the horn from the lower sac, except in so far as the ribs emerge from the horn, and there is a faint groove corresponding with the line along which the two divisions of the left side are apposed. The perforations mentioned above give the dorsal wall of the bladder an alveolate appearance, and indeed they are alveoli (Plate 4, fig. 2). The tissue between the openings is solid and extends medially to the vertebrae, dorsally to the outer wall of the bladder. Each alveolus is lined with *tunica interna*, and there are from six to eight such pits (on both sides or only one, depending on the size of the specimen).

The significance of these differences has yet to be determined. Two possibilities present themselves. One is that the difference is a sexual one (the two large fishes were definitely females, the smaller one probably a male), the other that the swimbladder changes with growth. If the latter is so, then the condition on the left side in large fishes requires a quite considerable reorganization of tissues, including the delamination of the floor to the dorsal horn so as to form a roof for the lower chamber, and the closing of the alveoli to complete the floor to the horn. I am inclined, in view of these rather complex changes, to favour the idea of there being some sexual dimorphism in swimbladder anatomy ; this point can easily be checked by examining several fishes of known sex.

As mentioned above, the oblique transverse wall provides an almost complete division between the single lumen of the subspherical sac and the divided lumen of the thin-walled abdominal sac. Connection between the three lumena is by means of small, ventrally situated and adjacent apertures contained in a pocket of the wall which I have termed the common vestibule. If the wall is viewed from the front, a small transverse slit is seen in its base lying immediately behind the opening of the pneumatic duct. The dorsal lip of the slit is slightly thickened (Plate 3). This slit forms the entrance to the common vestibule. A small, near circular (U shaped in plan) opening placed at a slight angle to the midline lies just behind the lip ; the walls of the opening are somewhat thickened. This is the entrance to the left division of the abdominal sac and it lies in the left hand wall of the vestibule. The opening to the right lobe is another small hole with a thickened margin, the thickening being a continuation of that surrounding the other opening. Unlike the opening to the left division, that of the right lies transversely and is in the " posterior " wall of the vestibule ; the two openings make an angle of about 100° with one another.

An unusual structure is found on the floor of the subspherical sac. It is a moderately large, roughly ovoid body (the long axis transverse) arising from a nearly square base just in front of the opening to the pneumatic duct (Text-fig. 1). From its position relative to this duct, it could perhaps be referred to as an " epiglottis ". In two specimens, this body is erect and occupies the position shown in Plate 4 ; in the third fish, however, it lies in a different position, as if collapsed. The head now occludes both the opening to the pneumatic duct and that of the common vestibule (Plate 3).

I have examined some sections of the " epiglottis " ; unfortunately, the material is rather poorly preserved but at least some idea of its histological organization can be gained. The thick basal pad is composed of rather irregularly arranged dense collagen fibres, with a few elastic elements. The main body, including the ovoid head section has an inner core of cartilage, surrounded by a thick jacket of collagenous-elastic connective tissue. Next to the cartilage, the collagen fibres are irregularly arranged but the greater part of the jacket is composed of densely packed and concentrically arranged collagen fibres. Elastic fibres also occur but are relatively sparse and are irregularly arranged. The cartilaginous core is eccentric, there being a greater thickness of connective tissue on the right side of the " epiglottis " ; that is to say, at the broad end of the ovoid. In this broader zone, the area of looser tissue is considerably wider than the concentrically arranged part. No trace of muscle could be found in the body of the " epiglottis " ; a few, scattered fibres appear in the basal pad. Externally, the whole structure is covered by a thin, squamous epithelium.

Thus, it seems fairly certain that if in life the " epiglottis " is movable it is not activated by any intrinsic muscles.

The abdominal sac may now be considered. Externally it is a single structure, but posteriorly it is bilobed. Internally, however, the anterior portion is completely divided by a paramedial and vertical septum (Plate 3). Unlike the subspherical sac, the walls of the abdominal sac are relatively thin and invested by a coat of intrinsic musculature. The muscle fibres are arranged vertically and run from the dorsal midline of the bladder (or nearly so) to the ventral midline of the anterior unpaired portion, or to about half way up the median wall of each lobe in the paired portion. This thin layer of muscle is of uniform depth over the entire abdominal sac. If the abdominal sac is punctured it immediately collapses, whereas the subspherical sac retains its shape, such is the greater rigidity of its walls.

It is not at first obvious that the posterior part of the sac is indeed bilobed since the medial aspects of the lobes are closely applied and joined by strands of weak connective tissue. If, however, a blunt probe is inserted anywhere along the median sulcus and then gently moved in an antero-posterior direction, the two lobes are easily separated over the hind two-thirds of the sac. The anterior third is not divisible. Dorsally, each of the separate lobes is closely applied to the vertebral column and to the underside of the ribs. Anteriorly (*i.e.* in the region of the unpaired part) the dorsal relationships of the sac are more complicated and were described above (p. 382).

Each posterior lobe is a complete tube, with its own coat of superficial intrinsic muscles. Where the lobes fuse medially, the common wall thus formed gives rise to the median septum dividing the lumen of the unpaired anterior part. This septum is thick and consists of a middle layer of *tunica externa* sandwiched between the *tunica interna* which lines each division. Anteriorly, the septum curves dextrally to fuse with the transverse wall separating the subspherical sac from the abdominal sac slightly to the right of the mid line.

The volume and diameter of the anterior compartment with its posterior lobe are the same on right and left sides. Apart from the common vestibule, which links the openings to the left and right compartments, there is no other intercommunication between the two sides, at least in the abdominal region. Internally the walls of the two compartments differ somewhat. Throughout its length the lumen of the left division (in large fishes) is smooth, whereas in large and small fishes the dorsal wall of the right division is alveolate over its anterior half. In the small specimen, the dorsal wall of the left division is also alveolate (see above, p. 382). The dorsal and lateral walls of each division (in fishes of all sizes) are strengthened by numerous, close-set fibrous ramifications which break the otherwise smooth surface of the wall into many narrow and shallow clefts. These fibrous half-bands become broader and more widely separated over the posterior half of the bladder. Throughout, the *tunica interna* is very thin and there are no signs of heavy vascularization. This aspect, too, requires verification from histological sections and examination of fresh specimens.

The posterior limit of the abdominal cavity is formed, in the midline, by the greatly enlarged first anal pterygiophore. To this bony eminence is attached the median wall of each abdominal lobe. From this point posteriorly there is no median wall of *tunica externa*, the two caudal lobes being separated merely by a thin partition of *tunica interna*.

Comparison with Asian Species

Superficially, the two most obvious differences between the abdominal swimbladder of *N. afer* and that of the Asian species are the penetration of its wall by the first seven ribs, and the bilobed posterior portion. Internally, the differences are more numerous.

The subspherical sac of *N. afer* is homologous with the similarly named portion in the Asian species ; this area will be considered first. In both groups the postero-dorsal part of this chamber is produced backwards to form the two dorsal horns overlying the anterior portion of the other abdominal subdivision, the medially divided abdominal sac. Some variation in the extent of overlap seems to exist amongst the Asian species, it being greatest in *N. notopterus* (personal observations).

However, even in this species the horns are not as long as in *N. afer*. In no Asian species do the horns surround the proximal portions of the ribs ; indeed, the entire abdominal swimbladder lies ventral to them. Neither is there any direct communication between the dorsal horns and the underlying part of the medially divided abdominal sac, as is the usual condition on the right side in large *N. afer* and on both sides in the smaller fish I examined.

Even greater are the differences in the form of the transverse, oblique wall which, internally, separates the subspherical sac from the divided abdominal sac. In all Asian species this wall (the oblique septum of authors) is developed only on the left side, the right hand chamber of the abdominal sac being in direct and wide communication with the lumen of the subspherical sac. As in *N. afer*, the opening to the left chamber is directed dextrally, but there is no well-defined common vestibule, and no Asian species has an " epiglottis " or any similar structure. In these fishes, the pneumatic duct opens into the left-hand chamber, but in *N. afer* the opening is medial and before the common vestibule which surrounds the openings to the left and right hand compartments. These pronounced morphological differences suggest some correlation with differences in swimbladder function.

Whereas in *N. afer* the lumen of the subspherical sac is undivided (except for the low incursion of the vertebral column), in Asian species it is partially subdivided by a velum developed in the dorsal midline, apparently as a continuation of the median septum dividing the abdominal sac.

The posterior part of the abdominal swimbladder in all Asian species is, apparently, a single tube with a complete dorsoventral partition down the midline. Neither Bridge (1900) nor Dehadrai (1957) has reported a bilobed portion and I have been able to confirm its unity in *N. notopterus*. Dehadrai (*op. cit.*) illustrates a cross section through the posterior abdominal bladder, showing a common median wall (composed of *tunica externa*) which divides the lumen into two chambers ; it is continuous above and below with the *tunica externa* forming the outer wall of the bladder. By contrast, in *N. afer*, the posterior two-thirds of the abdominal sac is distinctly bilobed. Admittedly the medial faces of the lobes are closely applied to one another but loose connective tissue separates two complete and distinct walls.

The internal face of the abdominal sac is smooth in all Asian species ; the anterior portion is never alveolate as in *N. afer* (see above, p. 382).

(ii) *Caudal Section of the Swimbladder* (Plate 1)

As in Asian *Notopterus*, the caudal swimbladder consists of two lobes, separated medially by the anal fin supports. In *N. afer*, however, the bladder extends further caudad, reaching to the caudal fin origin.

Immediately after leaving the abdominal cavity, the bladder curves sharply downwards and then rises gently upwards so that its posterior third lies at a level slightly above the abdominal part. Over the anterior half of its posterior extent, the depth of the bladder is not noticeably less than that of the abdominal part. But further back the depth gradually decreases until in the last third it is about a fifth of the depth anteriorly.

Ventral diverticula are given off throughout the length of the caudal bladder, there being between 115 and 120 from each lobe in the three specimens examined. Each diverticulum has a relatively broad origin, but soon tapers to a narrow tube. As far as I can determine most diverticula end in a single, fine point, although some may be bifid. The position of the diverticula is such that the deep muscle bundles attached to the anal fin rays lie between and below them. Each diverticulum is covered by the superficial fin muscles and lies above an anal pterygiophore.

Internally, the lumen of each lateral lobe is smooth and roughly D-shaped in section, the convex wall facing laterally. Since the *tunica externa* of the medial walls of the abdominal bilobed bladder ceases at the enlarged first anal pterygiophore, the caudal continuations of these lobes have only thin *tunica interna* inner walls. The external tunic is present over the lateral face, but is somewhat thinner than that of the abdominal sac. The entire lateral face of the bladder is covered by a thin sheet of muscle which has both its insertion and its origin on the bladder ; small slips invest the ventral diverticula. This intrinsic swimbladder musculature is thickest anteriorly ; over the posterior part of the bladder it is reduced to a very thin sheet a few fibres in depth. The fibres of the muscle sheet are vertically disposed throughout its length.

Although there is no *tunica externa* on the medial face of either caudal lobe, the delicate *tunicae internae* of each side are separated medially by a thin but tough and fibrous membrane extending between the anal pterygiophores. Some communication exists between the two lobes. In the posterior half of the bladder there are small vacuities in the interpterygiophore membrane, interradial in position and situated a little below the roof of the lobe. Apparently the *tunica interna* does not cover the hole, but it must be stressed that this observation was made on preserved specimens where the tunic is fragile and easily torn. Similar interconnections occur ventrally and are more numerous. Indeed, except for a short anterior region there is a vacuity near the origin of each diverticulum. The apertures of the dorsal vacuities are larger than those of the ventral series.

From gross dissections of preserved specimens I get the impression that the epithelium lining the caudal lobes is not highly vascularized (c.f. Dehadrai's 1962 observations in *Notopterus chitala*).

Comparison with Asian Species

The major difference between the caudal prolongations in *N. afer* and the Asiatic species is their greater length in the former (see Johnels, 1954). In no Asian species do the lobes extend to the posterior tip of the body. Judging from published descriptions of Asian species, the caudal bladder extends to slightly beyond a vertical through the dorsal fin ; in other words, to a point about mid-way between the anus and the caudal fin origin. Because of the greater swimbladder length in *N. afer* there are many more ventral diverticula in this species (115–120 c.f. 14–18 for the Asian species ; Dehadrai, 1957). The diverticula are much narrower in *N. afer* and it appears that whereas bifid diverticula are the rule in Asian *Notopterus* this condition is rare in *N. afer*. Presumed connections between the left and right lobes are described for all Asian species where, as in *N. afer*, dorsal and ventral vacuities occur in the median wall. It seems likely that ventrally the vacuities in *N. afer* are more proximal in position, and that their distribution dorsally is more irregular. Differences also exist in the distribution of the superficial intrinsic musculature. Dehadrai (1957) figures an unspecified specimen (from its shape, *N. chitala*) in which the muscle covers the dorsal and lateral aspects of the abdominal bladder from behind the subspherical sac. Caudally this muscle deepens to cover the lateral aspects of the bladder but not its dorsal part nor the ventral diverticula. It terminates bluntly at a point above the antepenultimate branched diverticulum. In a specimen of *N. notopterus* I have dissected there is no intrinsic muscle cover on the abdominal section, and in the caudal part it fails to cover the dorsolateral as well as the dorsal parts of the wall ; its caudal extension is similar to that figured by Dehadrai (*op. cit.*). Bridge (1900) does not mention any intrinsic muscles in *N. borneensis*, but notes that " The dorsal and external walls of each caecum are invested by a strong aponeurotic membrane the outer surface of which receives the insertions of the inner margins of the fibrous septa separating the caudal myotomes ".

In *N. afer* the muscle extends much further dorsoventrally throughout the entire length of the bladder ; in the bilobed abdominal section it even extends beyond the ventral midline and runs up the lower part of the median bladder wall. Also, a slip from the main muscle body invests the lateral face of each ventral diverticulum.

(iii) *Cranial* (*Precoelomic*) *and Interconnecting Parts*

(Plates 1–3 and Text-fig. 1)

When viewed laterally (Plate 2; Text-fig. 1) the external surface of this section is clearly subdivided into three parts. Anteriorly there is an elongate, cylindrical portion (the lateral lobe of the auditory portion) from the somewhat swollen hind margin of which there arises a short, broad and anterodorsally directed process. A deep, narrow groove separates the cylindrical portion from the succeeding divisions which are shaped like a pair of slightly truncated and contiguous hemispheres separated by a deep and narrow groove. These hemispheres connect with the subspherical sac through a short duct of slightly narrower diameter than either the hemispheres or the subspherical sac. Ventrally these subdivisions are less marked. The lateral aspects of the two truncated hemispheres protrude well beyond the level of the auditory part and, but less markedly, beyond the side of the subspherical sac. In the region of the hemispheres the *tunica externa* is inserted along the dorsolateral margin of the vertebral column, thus encompassing the head of the first rib which emerges through the posterior hemisphere. The *tunica externa* of the auditory chamber inserts along the lateral aspect of the skull (prootic and opisthotic ridge, see p. 391) dorsally, and along the posterior vertical margin of the prootic anteriorly, whilst anteroventrally there is a slight union with the hind end of the parasphenoid. The ventral wall of this chamber, however, hangs well below the level of the basioccipital which it encloses.

Internally, the lumen of the double hemispheres reflects the external subdivisions since the two deep external grooves (one between the hemispheres and one between the auditory chamber and the anterior hemisphere) are represented by high ridges of fibrous tissue running from the vertebral insertion of the *tunica externa* to a low and broad ridge along the midline of the hemispheres (Plate 3). These vertical ridges are deepest ventrolaterally and also broadest because each bifurcates before joining the median ridge. Since the *tunica interna* lies across the upper part of each bifurcation, the base of the ridge is much broader than its upper part.

The auditory chamber can hardly be considered a paired structure even though its lumen is partially divided by the lower otic region of the skull which occupies a considerable part of its volume. Only at the extreme anterior tip of the chamber is the *tunica externa* attached to the base of the skull, thereby forming a small pocket on each side. Elsewhere, its ventral and lateral walls lie away from the skull. Two paired structures arise from each side of the chamber, the inferior and superior intracranial diverticula. The former are anterior prolongations of the *tunica interna* lining the auditory chamber ; each enters the skull through a large foramen between the prootic and basioccipital of its side. Each superior diverticulum is a large, and subdivided, vesicle of *tunica interna* which leaves the posterodorsal part of the auditory chamber through a short duct whose origin lies immediately in front of the internal ridge dividing the chamber from the first hemisphere. These intracranial parts of the swimbladder are discussed later (p. 389).

Although the lateral and ventral parts of the auditory chamber consist of soft tunics, the dorsolateral portion is bony, being a deep, ventrally directed channel formed mostly from the basioccipital but partly by a thin ridge of prootic and opisthotic. Within the upper part of this channel lies the auditory fenestra, an extensive elliptical hole bounded by the prootic, opisthotic and basioccipital, and closed by a thin, very flexible membrane. Since the lower boundary of this fenestra is formed from the basioccipital (in this region, rather inflated) its axis is not vertical but slopes mesially at about 5° from the vertical. The thin *tunica interna* of the auditory chamber is closely applied to the skull region encased by the chamber and thus it comes into intimate contact with the fenestral membrane.

From the anterior, pocket-like corner of the chamber on each side of the skull, a broad finger of *tunica interna* passes obliquely through the prootic-basioccipital foramen and then runs forward intracranially (Text-figs. 1 and 2). This is the inferior intracranial diverticulum. It occupies a chamber in the inflated prootic and pterosphenoid, and ends bluntly just anterior to the pterosphenoid-orbitosphenoid union. The right and left diverticula are separated medially by a thin bony partition formed from the parasphenoid, prootic and pterosphenoid. No intercommunications were discovered.

The other paired intracranial diverticula are superior in position and arise on each side from the posterior part of the auditory chamber (see above, p. 387 and Text-figs. 1 and 2). A short duct, closely applied to the posterior face of the skull, leads from the chamber to the vagus foramen ; its lateral and posterior walls are of *tunica externa*, but the anterior wall is provided by the skull. The *tunica interna* lining the duct enters the skull through a short, narrow foramen in the exoccipital bone, separated from the vagus foramen only by a thin bony partition. Once within the cranium, this tube of *tunica interna* expands to form a spacious, near ovoid vesicle, whose walls are closely applied to a similarly shaped chamber lying above the ear and posterior parts of the brain (see section on skull, p. 391). Because of various projections from the walls and roof of this cavity, the lumen of the vesicle is rather irregular. Each vertical semicircular canal passes through the vesicle of its side and the horizontal canals are contained within the bony floor of the capsule. No septum separates the vesicles which are in broad contact mesially. The anterior wall of the cavity housing these vesicles is very thin but bony. It is deeply indented so as to form a broad V whose apex is directed caudally. On each side of the apex is an irregular perforation (sometimes nearly circular, sometimes a notch) situated in the upper part of the wall. The vesicles extend through the aperture of their respective sides and then expand again to form smaller anterior chambers each shaped like a dorsoventrally flattened ovoid. In alcohol-preserved specimens the anterior vesicles are separated by a near-membranous, slightly bony median septum ; no trace of this wall can be found in the dried skull.

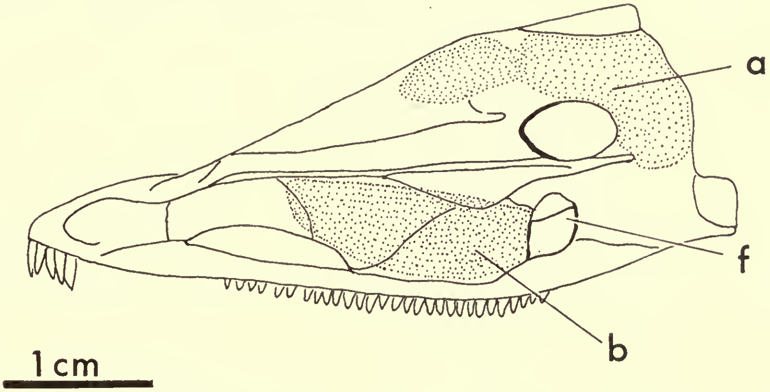


FIG. 2. *Notopterus afer :* lateral view of neurocranium to show position and extent of the intracranial swimbladder diverticula.
a : superior diverticulum ; b : inferior diverticulum ; f : foramen through which the inferior diverticulum enters the neurocranium.

Some measurements of these intracranial cavities were made from a dry skull ; since the *tunica interna* of the swimbladder vesicles is closely applied to the cavity wall, the figures also give some idea of the volume of the vesicles.

Total skull length . .	47·0 mm.
Posterior division of the superior cavity (left side)	
Greatest length . . .	13·0 mm.
Greatest depth . . .	7·3 mm.
Greatest width . . .	7·0 mm.
Anterior division of the superior cavity (left side)	
Greatest length . . .	10·0 mm.
Greatest depth . . .	4·0 mm.
Greatest width . . .	6·0 mm.

From the above descriptions it will be seen that in *N. afer* the inner ear is not only in contact with the swimbladder (*via* the lateral auditory chamber and the auditory fenestra) but it is also overlain by diverticula from this organ. Anteriorly the inferior swimbladder diverticulum wraps around the saccular part of the ear, which is only free from such associations on its medial side where the thin walls of the otic capsules are fused.

Comparison with the Asian Species

It is in the cranial portion that the swimbladders of African and Asian species show the greatest anatomical divergence. No Asian species has any intracranial division of the swimbladder, the auditory chamber is entirely extracranial. In very distinct contrast *N. afer* has not only a somewhat larger extracranial chamber but intracranial diverticula as well, the latter filling the posterior dorsal third of the skull and, at a lower level, extending forward to the orbit. A consequence of these diverticula is a marked difference in the neurocranial architecture of *N. afer* (see p. 392).

The relationship of the swimbladder and the sacculus is identical in both groups but there are differences in the form of the entire auditory chamber. For example, no Asian species shows the two anterior hemispheres which link the auditory and anterior abdominal parts of the bladder in *N. afer*. Instead, there is a very short and narrow portion connecting the subspherical sac with a slightly deeper anterior section which Dehadrai calls the " anterior prolongation of the subspherical sac ". Presumably Dehadrai based his observations on *N. chitala* because in a dissection of *N. notopterus* I find that this prolongation has a much greater depth (almost that of the subspherical sac) than he figures. In fact, its general shape is similar to that of the lateral and ventral auditory chambers in *N. afer*. The illustration of *N. borneensis* given by Bridge (1900) is almost identical with Dehadrai's (1957) figure of *N. chitala*. He describes the anterior prolongation in both species as "Tubular " in contrast to " Rounded, flask-like " for *N. notopterus* (Dehadrai, *op. cit.*). This part of the bladder is not entirely homologous with the joined hemispheres of *N. afer*, for although it is preabdominal in position it is partly attached to the skull. It seems therefore, to correspond to the posterior, slightly swollen portion of the auditory chamber in *N. afer*. In this species the auditory chamber is not a paired structure, but in Asian species paired processes arise from the " anterior prolongation of the subspherical sac "; these diverge from one another to constitute the anterior, truly auditory portion of the swimbladder. Their homologues in *N. afer* would seem to be those parts of the lateral walls of the auditory chamber overlying the auditory fenestrae. In Asian species the *tunica externa* of the true auditory caecum is inserted onto the skull both dorsally and ventrally so as to form a complete tube. *Notopterus afer* has the *tunica externa* of the auditory chamber inserted onto the skull only along its anterior and dorsal margins, the ventral part hangs below skull level (forming the ventral auditory chamber) thus making it impossible to consider the auditory portion of the swimbladder as truly paired.

THE SKULL OF *NOTOPTERUS AFER*

(Text-fig. 3)

Mention was made above of the effects which the intracranial vesicles have on neurocranial architecture. These will be described below in relation to the neurocranium of *N. notopterus* which Ridewood (1904) has described so painstakingly (Text-figs. 3 and 4).

Superficially, the neurocranium of *N. afer* gives an immediate impression of fragility and inflation, particularly in those areas associated with swimbladder diverticula. Since the superior intracranial vesicles are the largest, it is the upper part of the posterior neurocranium that differs most from *N. notopterus*. The periotic region will be considered first. The *opisthotic* is bullate, especially behind. Its ventral face is marked by two deep pits, of which the anterior is deeper and directed posteriorly. In preserved specimens these pits are lined with pockets of *tunica interna* developed from the lateral auditory chamber. Neither pit connects with the superior intracranial vesicle.

The *prootic* is somewhat more bullate than in *N. notopterus*, but the *sphenotic* is much inflated, particularly in the anterior region. By contrast, the *pterotic* is little affected by the general inflation of the otic region. The *epiotic* is greatly inflated so as to become a low cone. In *N. notopterus* this bone is compressed and in transverse section has the shape of an inverted J.

The *exoccipital* shows the greatest inflation of all the skull elements; no aspect is flat and its posterior face (except for a small dorsomedial depression) is strongly convex. In *N. notopterus* there are no convex surfaces and, when viewed dorsally, this bone is V shaped, with the apex facing anteromedially ; thus, its posterior aspect is strongly concave. The *foramen magnum* in *N. afer* is depressed and the exoccipitals meet above it in a deep vertical articulation, quite unlike the union in *N. notopterus* which is reduced to a point of contact above the triangular *foramen magnum*.

Other Neurocranial Elements

The *supraoccipital* is slightly broader in *N. afer* and its median crest is greatly reduced. The *parietals* are more domed, as are the *frontals* which meet in a rounded, broad ridge ; in *N. notopterus* the frontals meet in a thin, knife-edge ridge. The anteriorly directed frontal ridge which delimits the medial border of the supraorbital sensory channel is much broader in *N. afer*. The direction, depth and arrangement of the sensory canals do not differ markedly in the two species.

The *parasphenoid* differs slightly in that the posterior ascending part (which is preotic in position) is not so definitely a dorsally directed projection as it is in *N. notopterus ;* its union with the prootic is along a somewhat dorsally sloping articulation. This part of the bone is inflated so that with the bullate portion of the prootic it forms a noticeable preotic swelling.

The *basioccipital* in the two species is not noticeably different (except that in *N. afer* it shows the papery consistency that so characterizes the skull bones of this fish). However there is no lateral union of the basioccipital and prootic in *N. afer*. Instead, what should be the area of junction is opened out to form the large foramen through which the inferior swimbladder diverticulum enters to the skull. Above this foramen the prootic and basioccipital are joined by a small and rather weak area of contact. The *auditory fenestra* has the same relations in both species ; it is perhaps relatively more elongate in *N. afer*.

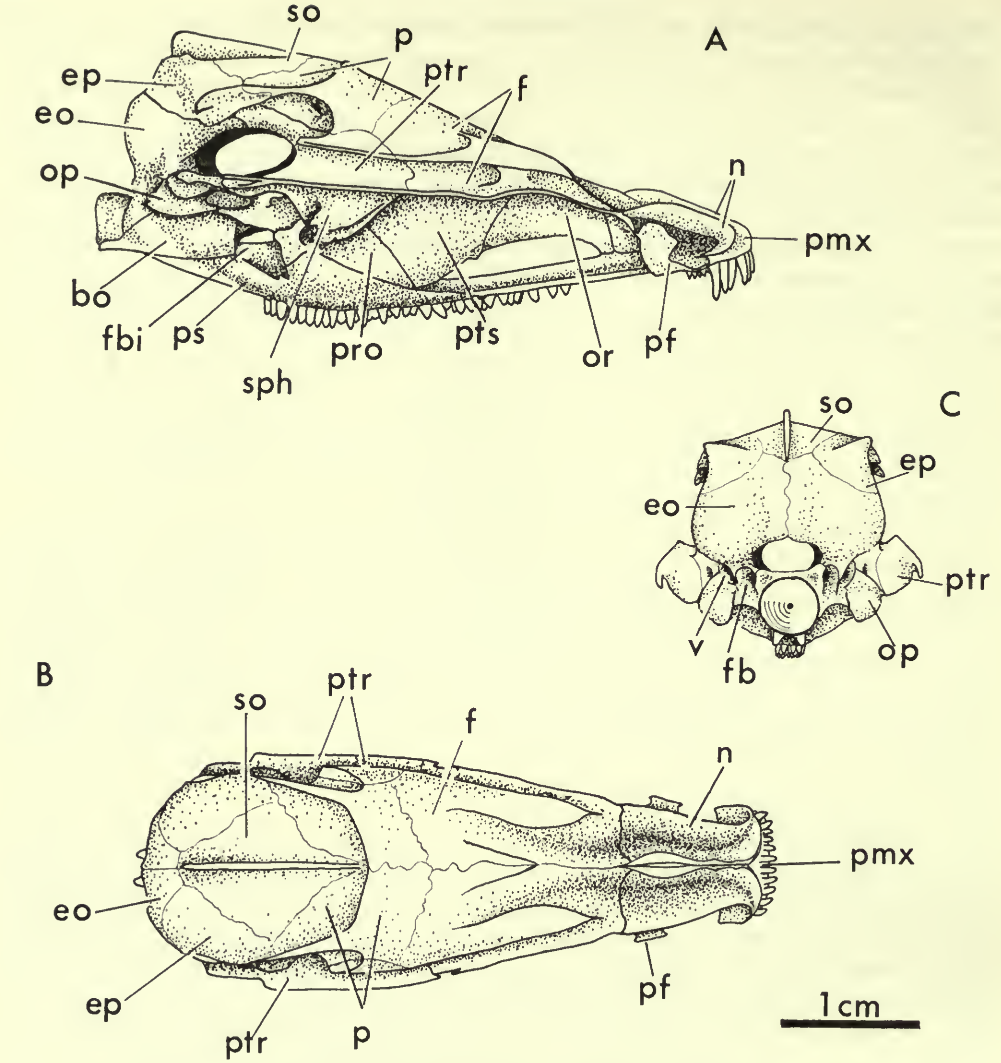


Fig. 3. *Notopterus afer* : neurocranium

A. Lateral view. B. Dorsal view. C. Posterior aspect. bo : basioccipital ; eo : exoccipital ; ep : epiotic ; f : frontal ; fb : foramen for swimbladder duct leading to the superior intracranial vesicle ; fbi : foramen for inferior intracranial swimbladder diverticulum ; n : nasal ; op : opisthotic ; or : orbitosphenoid ; p : parietal ; pf : prefrontal ; pro : prootic ; ps : parasphenoid ; ptr : pterotic ; pts : pterosphenoid ; so : supraoccipital ; sph : sphenotic ; v : vagus foramen.

The *pterosphenoid* is greatly inflated, both laterally and ventrally, so that its lower, curved margin almost reaches to the level of the parasphenoid ; midventrally, the left and right halves barely meet behind the orbitosphenoid. The orbitosphenoid is very bullate ; like the pterosphenoid it reaches far ventrally so that the space between these two bones and the parasphenoid is greatly reduced.

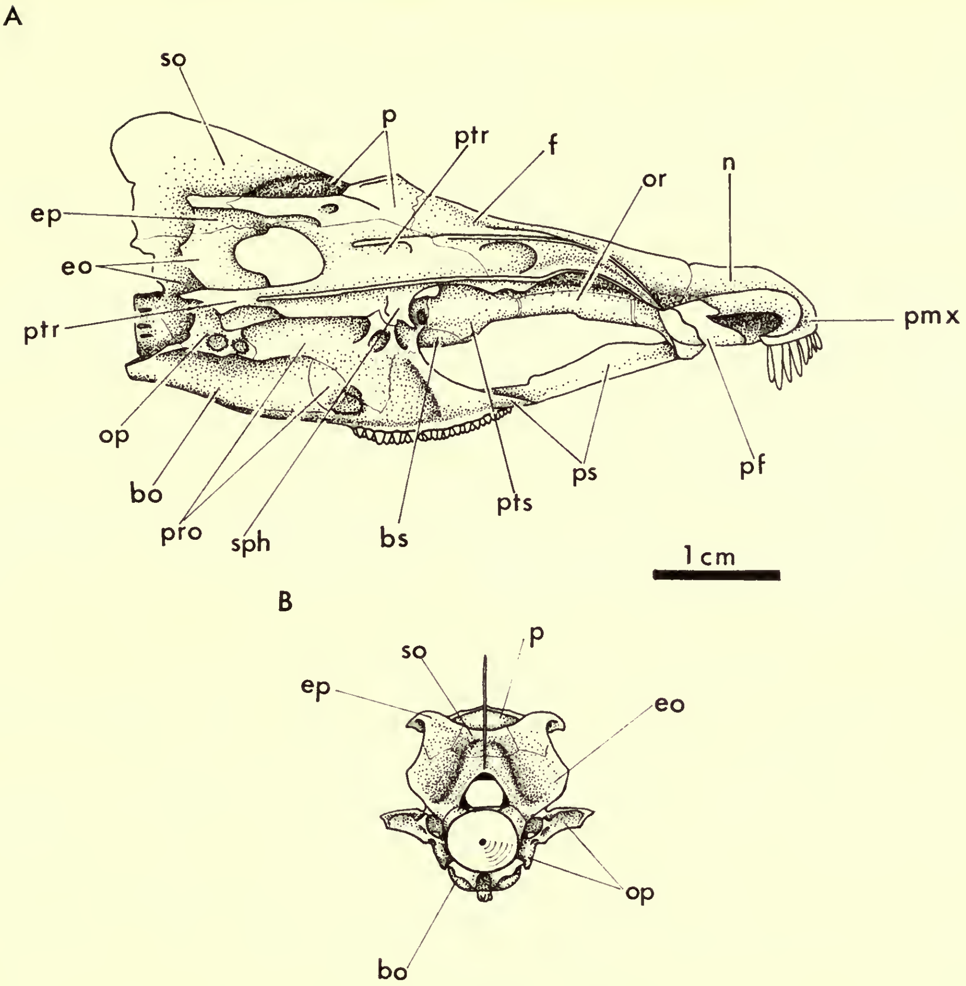


FIG. 4. *Notopterus notopterus*
A. Lateral view of neurocranium ; bs : basisphenoid ; all other abbreviations as in Text-fig. 3. B. Posterior aspect.

The *basisphenoid* is very small and is in contact with the parasphenoid. In a small skull I was uncertain whether or not this bone was present.

All the markedly bullate bones, or portions of bone, mentioned above have a characteristically pitted appearance ; in a dried skull many pits are perforated.

The bones forming the anterior part of the neurocranium do not differ greatly in *N. afer* and *N. notopterus*. Likewise, the *circumorbital, maxillary, mandibular, hyo-palatine* and *opercular* series of the two species show no fundamental differences. In *N. afer* only the lower margin of the preoperculum is serrated whereas in *N. notopterus* the lower circumorbitals and the edges of sensory canal gutters in the dentary and upper preoperculum are all strongly serrated.

There is a slight difference in mesopterygoidal dentition. *Notopterus notopterus* has an elongate, narrow patch of enlarged teeth running slightly lateral to the medial margin of the mesopterygoid, and a small patch of minute teeth on the main surface of this bone. *Notopterus afer* has no medial strip of teeth and the minute teeth on the main surface cover almost the entire bone.

Ridewood (1904) noted the presence of a separate opisthotic limb on the *posttemporal* of *N. afer* (absent in *N. notopterus*) but he did not comment on the epiotic limb which is also present, again in contrast to *N. notopterus*.

The *supratemporal* in *N. afer* is larger and less scale-like than in *N. notopterus* ; anteriorly it has a moderately large, backwardly directed and wing-like projection. A much smaller, spur-like projection is present near the posterior margin. A short segment of lateral line canal traverses the anterior dorsal angle of the bone ; it is continuous with the parietal canal.

The *hyobranchial* skeleton is similar in both species ; I count eight branchiostegal rays, but Boulenger found only seven.

Since the skull of *N. borneensis* is like that of *N. notopterus*, apart from its greater lateral compression, it follows that the skull of *N. afer* differs from it in exactly the same characters but with the general inflation relatively more marked. I have been unable to compare the skull of *N. chitala*.

THE SWIMBLADDER OF *XENOMYSTUS NIGRI*

No description of the entire swimbladder in *X. nigri* exists, although Müller (1950) has published a detailed analysis of muscles in the pneumatic duct.

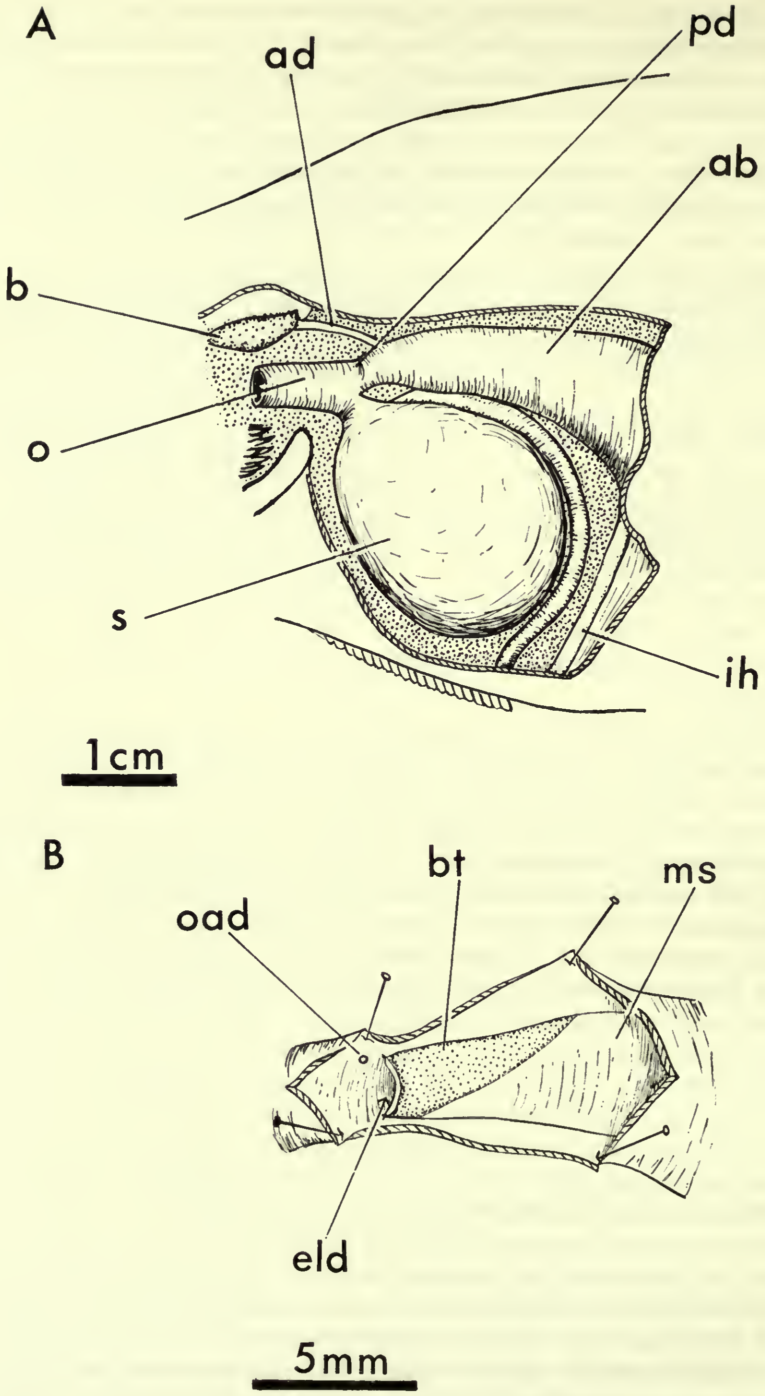
As in *Notopterus*, the swimbladder can be subdivided into cranial, abdominal and caudal parts. The anterior abdominal and the cranial parts are, however, very unlike those of *Notopterus*, as can be seen immediately on dissection (Text-fig. 5A). Whereas in *Notopterus* a large tube runs along the dorsal length of the abdominal cavity, in *Xenomystus nigri* the swimbladder seems to arise from the pneumatic duct as a posteriorly directed tube of moderate proportions. Near the posterior limits of the cavity the tube suddenly deepens so that its lower margin reaches almost to the ventral limit of the abdominal cavity. Throughout its length, the abdominal part of the bladder is a single structure. No anteriorly directed process connecting the cranial and abdominal parts is immediately visible. Further dissection reveals a narrow, slightly curved duct running from the dorsal surface of the main abdominal bladder towards the head (Text-fig. 5A) ; over most of its course the duct is embedded in kidney tissue. Close to the skull, the duct forks into two very short branches each of which is attached to the skull base. In contrast to the abdominal sac of *Notopterus*, that of *Xenomystus* is very thin-walled. The narrow duct, however, is thick-walled. It will be recalled that in *Notopterus* the anterior abdominal bladder has a much thicker wall than the posterior portion.

The caudal section is strikingly similar to that of *Notopterus* (especially the Asian species) and is provided along its whole length with ventral caeca, strictly interradial in position and reaching almost to the ventral margin of the body. Few caeca bifurcate distally. There are 70–75 caeca in the four specimens examined. As in

Notopterus, the deep muscles of the anal fin lie between and below the caeca, which are covered laterally by superficial fin muscles. The caudal division extends posteriorly to a point about two-thirds of the length of the post-abdominal body. In a fish 154 mm. S.L., the caudal bladder is 72 mm. long and the post-abdominal body 116 mm. long. The greatest depth is at the anterior end, the depth decreasing regularly thereafter. At the midpoint, the depth is less than half that at its origin ; from here posteriorly the depth diminishes rapidly until the last third of the bladder is little more than a narrow tube.

The intrinsic musculature is confined to the caudal bladder where it forms a well-developed sheet running along its entire length. It covers the lateral wall of the bladder except for a narrow dorsal strip extending outwards from the midline ; the ventral diverticula are not invested with muscle (c.f. *Notopterus afer* where each is partially covered by a small muscle slip). The muscle fibres are vertically arranged and the entire sheet is supplied by large branches of the eighth spinal nerve. I have dissected four specimens and find that in two the muscle sheet is markedly thicker than in the others where, in fact, it was difficult to distinguish. Unfortunately none of these specimens is well preserved and I could only sex one fish, a male. This has a thin muscle sheet. Perhaps some sexual difference does exist. Size can certainly be eliminated because all four specimens were of approximately the same length. Whether the muscle is relatively thick or relatively thin it is thickest over the anterior three-quarters of its length and becomes very thin near its posterior end.

The cranial part of the swimbladder is short. It consists only of the two anterior forks of the auditory tube, and the paired lateral auditory divisions. Each fork inserts onto a circular rim of bone which surrounds the opening to the auditory chamber of its side. In *Xenomystus* the auditory chamber is of a somewhat different nature from that of *Notopterus* since its walls are entirely bony. *Notopterus* has the lateral and ventral walls formed from the tough *tunica externa* ; in the African species there is a common ventral lumen but in the Asian species the chamber of each side is more nearly a separate entity. This process of separation has gone furthest in *Xenomystus* because the lateral and ventral walls of each chamber are replaced by bone (see section on the skull, p. 399). Thus, the chambers are converted to moderately elongate bony blisters situated on the ventral skull surface. Each opens posteriorly by a small, medially directed pore. If the bony lateral wall of a chamber is removed the underlying auditory region of the skull is virtually identical with that of *Notopterus*. That is to say, the lateroventral wall is formed by the slightly swollen basioccipital and, anteriorly, by a contribution from the prootic ; dorsally there is a downward facing gutter formed from the prootic (mainly) and opisthotic. Between the upper margin of the basioccipital and the lower, medial margin of the gutter lies an auditory fenestra, closed by a flexible membrane. Relative to the fenestra in *Notopterus*, that of *Xenomystus* is much larger. If the region just described is considered homologous with the lateral auditory chamber in *Notopterus* (particularly the Asian species) then there is also a short intracranial continuation of the swimbladder lodged within the inflated ascending arm of the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parasphenoid. The intracranial projection is subspherical and partially closed off from the auditory chamber by a downward projection of the parasphenoid. As in *Notopterus*, the auditory chamber is lined with *tunica interna* and is thus in close contact with the membrane closing the auditory fenestra.

In essence the swimbladder-auditory linkage in *Xenomystus* is like that of *Notopterus*, except that it is effected through a much narrowed prolongation of the abdominal swimbladder subdivision. The intracranial diverticulum is very slight in comparison with *N. afer*.

The Internal Structure of the Abdominal and Caudal Subdivisions

Little further need be said about the narrow tube connecting the auditory chambers with the main abdominal subdivision. It is of uniform diameter and arises slightly to the right of the midline and a little posterior to the distal opening of the pneumatic duct. The latter is remarkably broad and muscular (see Müller, 1950) ; its distal opening is marked by a strong sphincter behind which the main abdominal bladder expands slightly and then continues for a short distance before beginning to deepen again. Throughout its abdominal length the swimbladder is a single structure but it is divided internally by a thin, median partition running from just behind the origin of the tubular auditory connection to the enlarged first anal pterygiophore (i.e. the median posterior boundary of the abdominal cavity). The septum extends from the dorsal to the ventral wall of the bladder and is imperforate (Text-fig. 5B). Its anterior margin is thickened and somewhat bowed, the convex surface facing to the left. Immediately behind this lip an elongate and triangular bony plate is embedded in the septum ; its anterior edge extends from floor to roof of the bladder and its length is at least half that of the entire median septum (see Text-fig. 5B). The exact nature of the plate and its function have still to be demonstrated. But, from Benl's observations on captive *Xenomystus*, it may be connected with sound production (Benl, 1959).

The lumen of the abdominal bladder is quite smooth and, superficially, shows but slight vascularization.

In all essential details the internal structure of the caudal subdivision is like that of *Notopterus*. I could find no interconnecting vacuities in the dorsal part of the median wall. Ventrally, however, there is a vacuity near the distal end of each caecum except possibly those in the posterior third of the bladder. From preserved specimens it is impossible to determine the extent of superficial vascularization in the caudal subdivision.

FIG. 5. *Xenomystus nigri*

A. Lateral view of abdominal cavity to show the swimbladder and its auditory connection. B. Portion of swimbladder (viewed from left) to show the median septum with the bony triangle embedded therein. The left-hand wall of the bladder has been cut and the edges reflected.

ab : abdominal section of swimbladder ; ad : auditory duct ; b : bony plate covering lateral aspect of auditory chamber ; bt : bony triangle embedded in the median septum ; eld : entrance to right-hand division of the abdominal swimbladder ; ih : first anal pterygiophore ; ms : median septum ; o : oesophagus ; oad : opening of auditory duct ; pd : pneumatic duct ; s : stomach.

THE SWIMBLADDER IN *XENOMYSTUS* AND *NOTOPTERUS* COMPARED

The swimbladder of *Xenomystus* shows a mixture of *Notopterus*-like characters with others unique to the genus. In both genera the caudal portion is basically similar ; its shape and size in *Xenomystus* is intermediate between the African and Asian *Notopterus* species. The posterior abdominal portion (i.e. the bladder behind the opening of the pneumatic duct) is nearer the Asiatic *Notopterus* type, but it shows a general simplification of internal structure since its only internal division is a longitudinal one. The bony triangle in the median septum is unique.

It is in the anterior abdominal and cranial subdivisions that *Xenomystus* differs most markedly from *Notopterus*. In the latter genus there is a wide connection between the auditory and abdominal subdivisions whereas in *Xenomystus* the connecting link is reduced to a narrow duct ; the auditory chambers are also greatly reduced in volume. In *Xenomystus* the lateral wall of each auditory chamber is a sheet of bone which converts the chamber into a bony, extracranial bulla. The swimbladder-sacculus connection is identical in both genera.

As regards intracranial diverticula, *Xenomystus* shows a slight advance over the Asian *Notopterus* since there is a small inferior diverticulum anterior to the sacculus. This is, however, smaller and much less extensive than the comparable diverticulum in *N. afer* and there is no trace of an upper vesicle.

Although intergeneric differences in swimbladder detail are striking, the overall " bauplan " of this organ in *Xenomystus* is clearly stamped with the notopterid mark.

THE SKULL OF *XENOMYSTUS NIGRI*

Fundamentally, the skull of *X. nigri* is similar to that of the various *Notopterus* species. In certain details it combines characters of both Asian and African *Notopterus*, in others it is unique.

Neurocranium. The outline of the neurocranium differs from that of *Notopterus* in having a convex parasphenoid margin and the otic region rising at a much steeper angle. In this respect it is similar to *Hiodon* (see Ridewood, 1904).

The *etho-vomerine* and nasal regions do not differ from *Notopterus*. The frontals are rather more like those of *N. afer* than the Asian species. The *supraoccipital* is small, its crest reduced and its basal part slopes downwards and backwards unlike the near horizontal position it has in *Notopterus*.

The periotic region. The *prootic* is not markedly bullate except anteroventrally where it meets the ascending parasphenoid limb. I found some difficulty in determining the limits of the *opisthotic* ; apparently it has the same proportions and relationships as in *N. afer*. The *sphenotic* is small and not inflated. There is an extensive *pterotic*, like that of *Notopterus*, but differing in having the middle section of its supraorbital sensory canal roofed over. The *epiotic* shows some inflation and in this respect is about intermediate between the conditions found in *N. afer* and *N. notopterus* ; it has a concave posterior face as in *N. notopterus* but the depression is relatively shallower. The epiotics do not meet above the *foramen magnum* but are separated by a small wedge of supraoccipital. The *basioccipital* is moderately bullate over most of its length and fairly sharply constricted near its posterior end immediately before the condyle. A ridge runs obliquely forwards and upwards from the posterior tip, passing immediately below the vagus foramen and then becoming continuous with a ridge developed on the ventral face of the opisthotic. In turn, this ridge joins another from the lateral face of the most dorsal part of the prootic. The ridges on the two latter bones face ventrally and are slightly concave. Together with the bones from which it arises, the ridge forms a ventrally directed groove on the side of the skull leading upwards and towards the auditory fenestra. It passes above the fenestra and then curves down around its anterior edge. A similar groove occurs in all *Notopterus* species and is the " ventro-lateral vacuity " of Ridewood (1904). However, unlike *Notopterus*, in *Xenomystus* there is also a flat, horizontal shelf developed along the ventrolateral margin of the basioccipital. This shelf runs onto the bullate floor of the posterior part of the parasphenoid ; thereafter it continues vertically upwards as the posterior margin of the ascending parasphenoid limb. The shelf eventually joins the upper ridge (see above). In effect these ridges form a complete wall around the auditory fenestra, situated at some distance from the actual opening. Firmly attached to the rim of this wall is a thin, tear-shaped concavo-convex sheet of bone. Thus on each side a lateral chamber is formed which encloses the otic region of the skull. Anteriorly each chamber ends bluntly within the swollen parts of the parasphenoid and prootic, whilst posteriorly it opens through a small downward and medially facing aperture. This arrangement contrasts strongly with that in *N. afer* where the lateral wall of the auditory chamber is formed from *tunica externa* and right and left sides of the chamber are in direct communication through the common lumen lying below the base of the basioccipital. I consider that the bony lateral cover to the auditory chamber in *Xenomystus* represents an ossification developed in the *tunica externa* of the swimbladder (perhaps during ontogeny?) and that only the margins of the chamber are derived from skull elements. The lower ridge along the basioccipital (not developed in *Notopterus*) may be derived from that bone since no line of union is visible between the ridge and the basioccipital itself. The fact that the bony cover is a single ossification (at least in adults) and that it is separable from the ridge delimiting the auditory chamber seems to argue against its derivation from the same periotic bones that contribute to the ridge. Most of the auditory chamber is extracranial but the anterior portion (that lodged in the prootic and parasphenoid) is truly intracranial. Although both portions are continuous a curved ingrowth from the ascending limb of the parasphenoid subdivides the lumen into unequal anterior and posterior parts, the latter being the larger.

The *auditory fenestra* has the same relationship to the periotic bones as in *Notopterus* but it is relatively larger.

Anteriorly, the *parasphenoid* differs but slightly from that of *Notopterus*, although the part passing through the orbit is narrower and has a distinct ventral curvature. Its teeth are fewer, relatively larger and extend over a greater length of the bone (almost its entire orbital part). Posteriorly there is a well-defined ascending limb (as in *N. notopterus* but not *N. afer*) which is inflated. The posterior ventral part of the parasphenoid is broad and slightly concave ; it does not extend far beyond the anterior margin of the basisphenoid.

The *orbitosphenoid* and *pterosphenoid* are inflated, especially laterally, and are more like these elements in *N. afer* than those of *N. notopterus*. Behind the orbitosphenoid the left and right pterosphenoids meet in a fairly extensive union. A small, vertically disposed *basisphenoid* is present. It has a short descending process which meets the ascending arm of the parasphenoid. There is no trace of a posterior myodome.

The *circumorbital, opercular, maxillary, mandibular* and *hyo-palatine* series are of a typical notopterid type. Serrations are present on the margin of the lower circumorbitals, the lower edge of the preoperculum and the margin of its sensory channel, and on the lower margin of the dentary. The interoperculum is greatly reduced and the operculum is relatively smaller than in *Notopterus*.

In the only dry skull available, the *hyobranchial* skeleton is badly damaged but as far as I can see, there are no obvious differences between it and the *Notopterus* type. From dissection I have been able to confirm the presence of paired ventral processes originating near the second basibranchials (a shared notopterid-mormyrid character).

The *posttemporal* is triradiate, with a short epiotic branch and a tubular middle portion ; I cannot find an opisthotic branch.

The *supratemporal* is moderately large and not essentially scale-like. It carries a short length of closed lateral line canal which runs into the parietal canal. In outline this bone is T shaped, with the vertical limb short and the horizontal one deep.

THE TAXONOMIC POSITION OF *NOTOPTERUS AFER* AND *XENOMYSTUS* WITHIN THE FAMILY NOTOPTERIDAE

Günther's original description of *Notopterus afer* deals only with superficial characters. On the basis of these he was certainly justified in separating the one African form as a distinct species. Succeeding authors have followed this arrangement and all have tacitly assumed that *N. afer* did not differ anatomically from its Asian congeners. However, in the light of what is now known about the swimbladder, the relationship of *N. afer* with *N. notopterus*, *N. chitala* and *N. borneensis* must be reviewed. Dehadrai (1957) has re-examined and compared the swimbladder in the three Asian species. His work shows that some interspecific differences do occur, but compared with the condition found in *N. afer* the Asian species form a relatively uniform group. Above all, none has intracranial swimbladder diverticula, yet extensive intracranial vesicles are a feature of the African *N. afer*. Also, the caudal part of the swimbladder in this species is considerably more extensive and the abdominal section has many unique characters (see p. 380). As might be expected from the intracranial invasion of the swimbladder, the neurocranium in *N. afer* differs considerably from that of any Asian species.

In view of these substantial differences it seems realistic to consider *N. afer* as representing a distinct genus, for which I propose the name :

Papyrocranus gen. nov.

Type Species : *Notopterus afer* Günther, 1868.

Diagnosis : A notopterid fish differing from *Notopterus* and *Xenomystus* in the presence of extensive intracranial vesicles from the swimbladder, in the presence of an "epiglottis" at the internal opening of the pneumatic duct, in having an almost complete transverse septum in the abdominal subdivision of the swimbladder, in having the posterior part of the abdominal swimbladder divided longitudinally into two separate lobes, in having the caudal swimbladder subdivision extending to the caudal fin origin, and in having the proximal parts of the anterior six or seven ribs enclosed within the swimbladder.

The name *Papyrocranus* is derived from the Greek *papyros*, paper-reed and *kranos* a helmet, and refers to the paper-thin roofing bones of the skull. I am indebted to my colleague Dr. Ethelwynn Trewavas for suggesting this most appropriate name.

Since these investigations have also disclosed new details in the anatomy and osteology of *Xenomystus*, its taxonomic status should also be reconsidered.

Xenomystus Günther, 1868

Type Species : *Notopterus nigri* Günther, 1868.

Anatomical characters in the swimbladder of *Xenomystus nigri* provide additional grounds for its separation from *Notopterus* and *Papyrocranus* at generic level. However, even in *Xenomystus* no different structures are involved, merely the relative development of various parts which one can consider as common to the basic notopterid plan. But, when the swimbladder anatomy is taken in conjunction with the other generic characters (reduced number of branchiostegal rays and absence of a dorsal fin) then the deviation of *Xenomystus* from *Notopterus* and *Papyrocranus* seems to warrant the separation of the two groups at a higher, probably subfamilial, level.

Thus, the subfamilies of Notopteridae can be defined as follows :—

Notopterinae : Dorsal fin present ; 6–9 branchiostegal rays ; auditory connection with swimbladder wide ; lateral and ventral walls of auditory chamber formed from *tunica externa*. Two genera, *Notopterus* (with three species) widely distributed in south-east Asia ; *Papyrocranus* (monotypic) confined to western Africa.

Xenomystinae : No dorsal fin ; three branchiostegal rays ; auditory connection with the swimbladder through a narrow duct ; auditory chamber completely encapsuled in bone ; median septum of swimbladder with a bony inset. A single genus and species, *Xenomystus nigri* from the Nile, Niger and Congo river systems of Africa.

It is clear that the African notopterids have evolved more extensively than their Asian relatives (even if Fowler's [1941] proposed subgenera are accepted). Despite this continental separation, the genera of Notopterinae have evolved within a fairly definite pattern, and one not fully shared by the Xenomystinae.

SWIMBLADDER FUNCTION IN THE NOTOPTERIDAE

The structure of the swimbladder in the Notopteridae suggests that the organ may have at least three functions other than its usual hydrostatic one : *viz.*, as a means of aerial respiration, as an accessory auditory organ and, as an instrument of sound production.

Dehadrai's (1962) experimental work on two *Notopterus* species has shown beyond doubt that in these fishes the swimbladder serves as a lung. Johnels (1954) has seen *Papyrocranus afer* gulping at the surface of an overcrowded aquarium, but there are no recorded observations of similar behaviour in nature and no detailed work has been done on the physiology of respiration in this African species. On anatomical and morphological grounds there is no reason to suppose that the swimbladder of *Papyrocranus* should not function like that of *Notopterus*. Unfortunately I was unable to study the vascular organization of the organ, nor could I get adequate histological preparations of the swimbladder epithelium to see if it is as highly vascularized as that of *Notopterus*. In *Notopterus* there are obvious modifications to the vascular system which ensure an adequate blood supply to the organ and a " short-circuited " return of oxygenated blood to the heart (Dehadrai, *op. cit.*). The function of the superficial swimbladder muscles in respiration has not been determined ; Dehadrai suggests that they may serve to expel gas from the bladder, but he was unable to distinguish an inhalent and exhalent cycle in aerial respiratory movements. However, the fish certainly expels bubbles of gas as it swims away from the surface (Dehadrai, *op. cit.*).

Observations on the respiratory habits of *Xenomystus nigri* are also confined to aquarium studies. Müller (1950) and Benl (1959) both record this species as taking air at the surface, an activity I can confirm from observations made in the well-oxygenated tanks at the Aquarium of the Zoological Society of London. Again, there is no physiological evidence that the swimbladder functions as a lung, but its organization certainly suggests such a rôle.

There are definite records of sound production by *Xenomystus nigri*. Benl (*op. cit.*) describes these noises as short, deep, grunt-, belch- or bark-like sounds emitted irregularly and generally as single sounds, rarely in groups of two or three. Some idea of their amplitude may be gathered from the fact that Benl could hear them at distances of six to eight metres from the aquarium. The biological significance of sound production in this species is unknown, but Benl gives evidence that strongly suggests some connection with reproductive activities. Structurally, the complex musculature and shape of the pneumatic duct (see Müller, *op. cit.*) probably have some influence over the quality and nature of the sound produced (see Benl, *op. cit.*). Perhaps the peculiar bony triangle embedded in the median septum of the swimbladder is also involved. It may act after the fashion of the reed in a wood-wind instrument. Doubtless the well-developed superficial swimbladder muscles are also involved in sound production, either to set up vibrations in the contained gas or even to expel the gas through the pneumatic duct.

There are no records of sound production in either *Notopterus* or *Papyrocranus*. Dehadrai (1957) suggests that the vertical hanging septum in the subspherical sac of *Notopterus* could act as a vibrator. No such septum exists in *Papyrocranus*, but the arrangement of openings to the paired abdominal sacs, the epiglottis and the pneumatic duct suggest a possible means of sound production (if gas is forced through them from the posterior part of the bladder, perhaps by contraction of the superficial muscles). The extensive and much branched caudal bladder may also be involved, acting as a resonater to the superficial muscles as vibrator.

No direct evidence has been obtained to show that the notopterid swimbladder has any role in hearing. The intimate association of swimbladder and auditory fenestrae (the latter in contact with the enlarged sacculus, see p. 388) does, however, suggest that acuity of hearing in the different species may be above that of fishes classed by Dijkgraaf (1960) as " normal ". Certainly the ear-swimbladder connection in Notopteridae seems, at least anatomically, to be as intimate and effective as that of the mormyrids and anabantoids, fishes which Dijkgraaf classes with the Ostariophysi as " specialists " in sound reception. Indeed, on anatomical grounds I would place the connection as being nearer the ostariophysine condition than that of the other two specialists mentioned.

THE HIGHER TAXONOMIC POSITION OF THE NOTOPTERIDAE AND THEIR RELATIONSHIP WITH THE HIODONTIDAE AND OSTEOGLOSSIDAE

Classifications of the order Isospondyli published during the past sixty years reflect the uncertainty of our knowledge regarding the interrelationship between the Osteoglossidae, Notopteridae and Hiodontidae, particularly the two latter families. In some schemes there is an implied relationship between the osteoglossids and the notopterids with the hiodontids more distant ; in others all three are grouped together. The clearest recognition of close affinity is found in the latest classification of isospondylous fishes (Gosline, 1960, 1961). Here the osteoglossids, notopterids and hiodontids are given superfamily rank and placed in the suborder Osteoglossoidei, itself forming one of the two divisions making the order Clupeiformes.

Gosline does not comment on the degree of relationship existing between the three superfamilies. Other workers (Regan, 1909 ; Berg, 1947 ; Norman, 1957) suggest closer affinity between the Hiodontidae and Notopteridae by grouping them in one suborder, and placing the Osteoglossidae in another.

Boulenger (1904) was one of the first authors to give detailed reasons for closely relating the hiodontids and notopterids ; he says : " The Fishes which form this family (Notopteridae) may be regarded as an eccentric modification of a type very similar to the preceding (Hiodontidae), with which they agree in most osteological features as well as in the dentition, in the connexion between the air-bladder and the ear, and in the absence of oviducts."

Ridewood (1904), basing his arguments on the swimbladder-ear connection and the cranial osteology, could not accept Boulenger's views. He cautions against the use of the swimbladder connection to imply close relationship, and found several osteological characters which he believed linked the Notopteridae rather more closely with the Mormyridae than with the Hiodontidae. Later, Marshall (1962) repeated Ridewood's view, with particular emphasis on the ear-swimbladder link, and amplified it thus " . . . . . . But a more significant point is that reliance can only be given to structures that are closely similar in all essential respects ". He goes on to express the view that Ridewood's description of the swimbladder in *Hiodon* suggests that it " is not *closely* like that of a notopterid. In fact the divergence seems substantial ".

In order to review these divergent opinions I have dissected the ear-swimbladder connection in two specimens of *Hiodon alosoides*, and reconsidered the osteological evidence. My conclusions are nearer Boulenger's than Ridewood's and Marshall's.

First, evidence from the swimbladder ; taken in its entirety, there are few points of resemblance between the notopterid bladder and that of *Hiodon*. The latter has a much simpler structure, lacks internal subdivisions and is confined posteriorly to the abdominal cavity. It is, however, divided into a partly thick-walled precoelomic (*i.e.* auditory) portion and a thin-walled abdominal part. The thick-walled auditory division is in the form of paired vesicles each intimately applied to the otic skull region of its side (dorsally to a ridge on the exoccipital, ventrally to a ridge sloping upwards and forwards along the basioccipital, and anteriorly to the vertical prootic lamina which bisects the auditory fenestra ; see Ridewood, 1904). Internally each vesicle is lined with *tunica interna* which, medially, is closely applied to the thin membrane occluding the auditory fenestra. Since the fenestra lies next to the upper part of the sacculus, the swimbladder has, in this respect, the same auditory relationships as in the notopterids. One major difference is in the divided nature of the *Hiodon* auditory fenestra and the associated tunics of the swimbladder. The vesicle of *tunica interna* does not extend forward below the prootic lamina but the *tunica externa* does seem to continue beyond the junction of the thickened, fibrous part with the underlying lamina. The anterior extension of *tunica externa* is thin-walled like the abdominal part of the bladder. It is attached to the prootic around the anterior margin of the auditory fenestra. When pressure is applied to the fibrous vesicle, the thin-walled part bulges outward and forward ; I have not been able to discover whether this anterior chamber is filled with fluid or gas. It could well be a lateral extension of the perilymph system.

If only that part of the precoelomic swimbladder lying behind the prootic lamina is considered then the auditory connection in *Hiodon* and the notopterids is " closely similar in all essential respects ". But the anterior chamber in *Hiodon* does not find a detailed parallel in any notopterid. The auditory fenestra is delimited by a slightly different arrangement of bones in the two families, but in each case it places the same part of the inner ear in contact with the swimbladder and it is in a comparable part of the otic region (see below). It could be argued that the sum of these characters is not *closely* similar in the two families. But it cannot be denied that they resemble one another in these respects more than either does the Osteoglossidae or any other isospondylous fish. Indeed, if a comparison is made with those members of the Clupei having ear-swimbladder connections one striking point emerges : namely, only in the Hiodontidae and Notopteridae is the connection effected through the lateral wall of the otic capsule. In Clupei an extension of the swimbladder enters the skull and forms one or two vesicles associated intracranially with the sacculus or utriculus. Such intracranial swimbladder diverticula as occur in *Papyrocranus* and *Xenomystus* are certainly not closely similar to the Clupei type.

If one restricts comparison of the hiodontid and notopterid swimbladders to the auditory connection, then the degree of similarity seems to equal that characterizing the group of Clupei which Marshall (1962) isolates as the division Clupeiformes (*i.e.* the families Clupeidae, Chirocentridae and Denticipitidae). Unlike Marshall's Clupeiformes, the Hiodontidae and Notopteridae differ from each other in the way the rest of the swimbladder is organized. *Hiodon* appears to have the more primitive type.

Turning to osteological characters one finds almost general agreement amongst authors that *Hiodon* is more primitive than *Notopterus* (and certainly *Papyrocranus*). However, neither Ridewood (1904) nor Gosline (1960, 1961) believes that the skeleton of *Hiodon* indicates a close relationship with the Notopteridae (see above, p. 403 for Ridewood's comments). The caudal fin skeleton (Gosline, 1960) requires little further comment. It is of a very primitive type and Gosline is unable to derive the notopterid or osteoglossid type from it (or for that matter from the skeletal type found in any living isospondylid). Neverthless, Gosline grouped *Hiodon* in the Osteoglossoidei because of other characters, principally the low number of caudal fin rays, the nature of its nasal capsule and its type of parasphenoid.

Ridewood (*op. cit.*) made a detailed study of the syncranium and concluded that *Hiodon* had more primitive characters than *Notopterus* and that he could not support Boulenger's views on the relationship of the two genera (see above, p. 403). Three characters most engaged Ridewood's attention—the swimbladder, the lateral cranial foramen with the associated supratemporal, and the paired bones articulated with the second basibranchial in *Notopterus*. I have considered the swimbladder already ; the osteological points will be discussed together with others which Ridewood did not consider.

The major neurocranial differences are as follows :— the absence of a lateral cranial foramen in *Hiodon*, the presence in this genus of a clupeid type of auditory fenestra, the membranous outer walls of the cephalic lateral line canals in the Notopteridae compared with the more typical complete bony tubes in *Hiodon*, and the very large canal-bearing supratemporal in that genus compared with the small canal-less bone in *Notopterus*.

In *Hiodon* there is a lateral cranial fenestra (Ridewood's cartilaginous tract), bounded by the parietal, pterotic and epiotic, which Ridewood homologises with the pre-epiotic groove in clupeids. He also suggests homology between the lateral foramen of notopterids (bounded by the pterotic, epiotic and exoccipital) and the pre-epiotic groove. Considering the relative enlargement of the pterotic in notopterids and the fact that the exoccipital has been somewhat displaced by the expanded opisthotic, it seems reasonable to consider the fenestra of *Hiodon* and the foramen of notopterids as homologous structures. The auditory fenestrae in the two families are not very dissimilar when considered as openings into the otic capsule, although the peculiar prootic lamina which divides the fenestra in *Hiodon* is a unique structure. That different bones delimit the aperture in each genus can also be ascribed to the different relative sizes of the otic bones in notopterids. In both these characters *Hiodon* would seem to represent the modern expression of a skull not far removed from a basic ancestral type which also produced (by differential growth of certain bones, possibly under the influence of the evolving swimbladder) a basic notopterid neurocranium.

The large supratemporal of *Hiodon*, which covers the parietal and a considerable part of the temporal region, certainly differs from the much smaller, scale-like bone of the Notopteridae. It should be noted, however, that the supratemporal of *Papyrocranus afer* is larger than that of *Notopterus* and *Xenomystus*, and that unlike the supratemporal of the former genus it carries part of the transverse parietal lateral line canal. Amongst the isospondyls as a whole the supratemporal shows great variation even within members of a suborder ; for example, the differences between *Elops* and *Albula* (Elopoidei) are as great as those between *Hiodon* and *Notopterus*.

Perhaps one should not attach too much importance to the supratemporal as an indicator of phyletic affinity. It is a bone which can be affected by numerous other systems (musculature, relative development of lateral line canals, fenestration of the neurocranium), and in the case of *Hiodon* and *Notopterus* is clearly affected by the marked differences in the cephalic lateral line systems. If anything, the latter might seem to provide a better indicator of phyletic divergence.

In *Hiodon* the cephalic lateral line canals (except the pterotic canal) are enclosed in perforate bony tubes. There is a well-developed parietal branch of the supraorbital canal but no transverse canal in that bone. Instead, the canal runs through the posterior margin of the supratemporal ; the posterior part of the supraorbital canal is also continued onto this bone. The pterotic canal has a bony roof but it is covered only by skin ventrally and laterally except for a short tubular portion posteriorly. Externally, the line of this canal is visible (at least in spirit specimens) as a faint, scaleless groove running immediately above the upper margin of the uppermost circumorbital bone and the operculum respectively. I have not been able to detect whether or not neuromasts are present in the open portion of the canal.

The Notopteridae have a very different system. All the canals, except the parietal transverse canal which is tubular, are deep open grooves, roofed over by skin (see also Omarkhan, 1949) ; none of these canals opens to the surface. The pterotic, parietal (*i.e.* transverse), preopercular and post-temporal canals have a common junction lateral to the cranial fenestra. This lateral line chamber suggests affinity with the " *recessus lateralis* " of clupeids (Wohlfahrt, 1936) although in notopterids the suborbital canal does not open into it and the membrane sealing off the perilymphatic space is stouter and sometimes covered by a fatty plug. It would be interesting to discover the physiological effects of such close association between the ear and the lateral line. The nasals in the two families also reflect the difference in canal structure ; in Notopteridae they are broad gutters whereas in *Hiodon* they are narrow tubes.

Although these differences in the lateral line system are both obvious and trenchant their value as pointers towards phyletic distinctness may not be so great. Indeed, they seem to indicate relationship of a degree comparable with that suggested by the skull and the swimbladder. Already in *Hiodon* there is the beginning of a notopterid-type of lateral line because the pterotic canal is not completely enclosed by bone and, perhaps of great significance, the lateral line system is in fairly close contact with the ear ; the pterotic canal is separated from the horizontal semicircular canal by thin bone. Omarkhan (*op. cit.*) drew attention to the correlation between enlarged cephalic lateral line canal systems and an association of this system with the ear. It is difficult to decide from the known examples whether the ear-lateral line connection is established first, or whether the canals enlarge and thus are brought nearer the ear. Be that as it may, *Hiodon* does seem to represent an early stage in the evolution of a notopterid pattern.

The jaw arrangement, especially the anterior articulation of the hyopalatine and maxillary series, is of a primitive type in hiodontids and notopterids. A similar arrangement is otherwise found only in the Osteoglossidae and Denticipitidae. This point is discussed later. The opercular series is complete in the Hiodontidae although the suboperculum is small (absent in Notopteridae) and the interoperculum hidden by the preoperculum, as it is in the Notopteridae. Again, the impression is that *Hiodon* represents an early stage in a trend culminating in the Notopteridae.

In the presence of paired tendon bones attached to the second basibranchial the Notopteridae differ from the Hiodontidae (but, as Ridewood notes, resemble the Mormyridae) ; there is no trace of these bones in *Hiodon*, merely paired tendons.

In both notopterids and hiodontids there are well-developed parapophyses fused to the centra, but the ribs are sessile and articulate with the vertebrae above and well behind the parapophyses. This is an unusual arrangement. In other isospondyls the ribs generally articulate with the parapophyses or, if sessile they lie immediately behind and below the weakly developed parapophyses when these are present.

There are other osteological differences between the two families but they are apparently of little significance from a phyletic viewpoint.

To sum up : the ear-swimbladder connection in the Notopteridae and Hiodontidae is basically similar and is of a kind not found in any other Isopondyli ; the condition found in *Hiodon* could be interpreted as representing an early evolutionary stage in a series leading through *Notopterus* to *Papyrocranus*, with *Xenomystus* as an independent off-shoot. Differences in neurocranial architecture seem explicable on the basis of differential growth in certain elements of the notopterid neurocranium (probably associated with the further evolution of the swimbladder-ear connection) ; again, *Hiodon* provides a basic plan, in this instance linking the notopterid condition with that of the clupeoids. The smaller supratemporal of the Notopteridae seems to be associated with the peculiar development of the cephalic lateral line system in that family ; the supratemporal is freed from its canal-bearing role by the development of a common lateral chamber from which radiate the canals usually carried by this bone. The cephalic canals of the notopterids are unique ; those of hiodontids suggest a very early stage in the evolution of such a system from a generalized type. The notopterids and hiodontids have a unique arrangement of ribs and parapophyses. Also shared by the two families (and the Osteoglossidae) is the simple anterior arrangement of the hyo-palatine and maxillary bones with the ethmoid region of the skull. Other osteological differences in the syncrania seem to be of little significance since they occur throughout the Isospondyli and cut across any system of classification. The caudal skeleton of *Hiodon* is a primitive and basic one, that of the Notopterids highly specialized ; however, Gosline is unable to derive the latter directly from the former.

Taking all these characters into consideration, I conclude that the Hiodontidae are more closely related to the Notopteridae than Ridewood (1904) or Marshall (1962) would concede. On the other hand, interfamilial divergence seems sufficiently great to warrant more recognition than that accorded by Berg (1947) or Norman (1957) who separate the two as families within a suborder. Phyletically, it seems correct to place the two groups in one suborder ; perhaps the best indication of their relationship is to give each group superfamily status. In this respect I agree with Gosline (1960), but I do not agree with his action of uniting the Hiodontoidae and Notopteroidae with the superfamily Osteoglossoidae in one suborder (Osteoglossoidei).

The hiodontids, notopterids and osteoglossids are, as Gosline (1960, 1961) has argued, a group readily distinguished from other isospondylous fishes and certainly warranting their segregation into a major division. Diversification within this line has, however, produced three distinctive end-points, two of which are more closely related to each other than either is to the third. This surely indicates that the common stock divided fairly early in its existence, or even its oligophyletic rather than strictly monophyletic origin. Following this reasoning, I believe that the relationships of the three groups are best expressed by uniting the notopteroids and hiodontoids in one suborder and placing the osteoglossoids in another. What status should then be given to the two suborders? Gosline (*op. cit.*) placed them in one Clupeiform division (Osteoglossi) and all other isospondyls in another, the Clupei.

To characterize the division Osteoglossi, Gosline has drawn on the following characters : the possession of a primitive parasphenoid, a parasphenoidal-glossohyal primary bite, the simple arrangement of the hyopalatine-maxillary-ethmoidal articulations (a most distinctive character of the group), peculiarities in the nasal capsule, the parapopheses well-developed and co-ossified with the centra and the low number of principal caudal fin rays ; to these may be added the nature of the swimbladder-ear connection when this is present. The sum of these various characters sets the division Osteoglossi well apart from the Clupei or any subdivision of the Clupei and it seems reasonable to give the division the formal status of an order (Osteoglossiformes), particularly since this step would emphasize more definitely the phyletic distinctiveness of the group. Gosline apparently did not take the step because he believes that orders and suborders should be interpreted rather broadly and not created for a few aberrant forms (Gosline, 1960). But, although the extant Osteoglossi are few in number, they are hardly aberrant. Rather they appear to be a not particularly successful evolutionary line developed from some pre-clupeoid stem. We know surprisingly little about the ecology of the Osteoglossi and it is thus difficult to suggest why they are an impoverished line. The jaw structure is certainly less flexible (from both the functional and adaptive view-points) than that of the Clupei and this may have been a restraining factor, as may have been their stenohalinity, for there is only one record of the group in marine deposits.

Judging from their anatomy the Osteoglossi are an ancient group. Since the two suborders are fairly well-defined and both possess unique characters unrepresented amongst living Isospondyli it is difficult to decide which group retains the greater number of " primitive " characters. The Hiodontoidae are, in most respects anatomically less specialized than either the Osteoglossoidae or the Notopteroidae yet the former retain the primitive parasphenoid-pterygoid articulation which is lost in the hiodontoids and notopteroids. Since this articulation may occur as a transient structure in the embryo *Salmo* (de Beer, 1927) its retention in the osteoglossoids may be an adaptive feature. None of the primitive living isodpondyls (*Elops*, *Albula*, etc.) provides a close link with the Osteoglossi. Surprisingly, it is with the recently discovered Denticipitidae (Clausen, 1959 ; Greenwood, 1960) that I find the most suggestive common characters, although the relationship, if any, is very distant in time as well as morphologically.

The Denticipitidae is a peculiar family of small freshwater and primitive Isospondyli, so far found only in Africa. The living species (*Denticeps clupeoides*, Clausen) occurs in a few localities in Nigeria and the fossil form (*Palaeodenticeps tanganyikae* Greenwood) from a presumed late Tertiary deposit in Tanganyika. Marshall (1962) has suggested a close relationship between *Denticeps* and the Clupeidae, mainly on the nature of the swimbladder-ear connection (which closely resembles that of *Clupea*) and the presence of opercular sensory canals. In other characters too *Denticeps* resembles the clupeids (e.g. the temporal foramen and the auditory fenestra). However, in having a short parasphenoid, simple hyopalatine-maxillary-ethmoidal relationships, enlarged, continuous gutter-like nasals, sessile ribs inserted behind the ankylosed parapophyses, the Denticipitidae shows Osteoglossiform characters. I do not suggest that the living (or recent fossil) denticipitids are close relatives of the Osteoglossiformes (nor for that matter do I support Marshall's close union of the Denticipitidae with the Clupeidae and Chirocentridae). Rather, I suggest that the modern denticipitids are survivors of a formerly more diverse denticipitoid group which, phyletically (and anatomically) speaking, connected the now divergent lines represented by the Osteoglossiformes and Clupeiformes. Much has still to be learned about the modern Denticipitidae and these suggestions are made from a relatively superficial acquaintance with the family. My main reason for disclosing them so prematurely is to bring attention to the family as a potentially important link in our speculations on the phylogeny of primitive Isospondyli.

At present it seems worthless to speculate further on the origin and affinities of the Osteoglossiformes. Nothing discussed above or that I have come across in my researches appears to invalidate the generally held view that the mormyroid fishes were evolved from some branch of the notopteroid-hyodontoid line.

A SYNOPSIS OF THE ORDER OSTEOGLOSSIFORMES

Order Osteoglossiformes

Maxillae without pedicels ; palatines end anteriorly in a simple point, without well-developed maxillary-palatine articular facet (the bones fused in *Pantodon*) ; no supramaxillae ; parasphenoid usually terminating well before the posterior limit of the basioccipital (*Scleropages* is exceptional), generally toothed (*Clupisudis* is exceptional), sometimes with a lateral process for articulating with the endopterygoid (Osteoglossoidei only) ; parapophyses well developed, ankylosed with the centra, ribs either articulating with the parapophyses or sessile ; nasal capsule rigid, without a mobile antorbital-supraorbital pumping device (supraorbital absent or fused with frontal) ; swimbladder-ear connection (if present) not of the clupeid type ; branched caudal fin rays 16 or less.

Two Suborders :

Suborder Osteoglossoidei : parasphenoid process for articulation with endopterygoid ; basisphenoid absent ; nasals enlarged, flattened, suturally united with the frontals and generally with one another (separated medially in *Pantodon*) ; no swimbladder-ear connection ; cephalic lateral line system contained in bony tubes ; ribs articulate with parapophyses.

Suborder Notopteroidei : no parasphenoid process for articulation with endopterygoid ; basisphenoid present ; nasals gutter- or tube-like, sometimes enlarged, sometimes meeting medially, never flattened or suturally united with frontals ; well-developed swimbladder-ear connection ; ribs sessile but parapophyses well developed.

Superfamily Hiodontoidae : separate uroneurals in caudal skeleton ; nasals tubular, separated medially ; cephalic lateral line system contained in bony tubes ; no lateral cranial foramen ; swimbladder not extending posteriorly beyond the abdominal region ; no median septum in swimbladder.

Superfamily Notopteroidae : no separate uroneurals in caudal fin skeleton ; nasals gutter-like, articulating with anterior end of frontals, and meeting one another dorsomedially in the midline (separated in ventral midline by fronto-mesethmoid ridge) ; cephalic lateral line system contained in bony gutters roofed with skin ; well-developed lateral cranial foramen ; swimbladder extending beyond abdominal cavity into caudal region ; median septum developed in swimbladder.

SUMMARY

The swimbladder of *Notopterus afer* is described. It differs considerably from that of the Asian *Notopterus* species, particularly in having voluminous intracranial diverticula and in extending posteriorly to the caudal fin base. The internal organization of the abdominal section is also markedly different, and includes an epiglottis-like structure situated above the entrance of the pneumatic duct.

Because of the intracranial swimbladder vesicles the neurocranium of *N. afer* differs from the type found in Asian species, being more bullate and the bone spongy.

When all these characters are considered it seems advisable to separate *N. afer* as a distinct monotypic genus for which the name *Papyrocranus* is proposed.

The swimbladder and skull of the other African notopterid, *Xenomystus nigri*, are described and compared with *Papyrocranus afer*. In this case the differences warrant the segregation of *X. nigri* in a distinct subfamily (Xenomystinae) ; *P. afer*

and the Asian *Notopterus* species are grouped together as the Notopterinae. Outstanding characters of the *Xenomystus* swimbladder are its narrow connecting duct between the auditory and abdominal parts and the thin bony plate developed in the internal median septum dividing the abdominal part. Only a small paired intracranial diverticulum is present ; the auditory diverticula of the swimbladder are encased in bone but are essentially extracranial in position.

The broader taxonomic position of the Notopteridae is considered, particularly in relation to the Osteoglossidae and Hiodontidae. It is concluded that the notopterids and hiodontids are fairly closely related to one another and that both are related to the Osteoglossidae. In general these conclusions are in agreement with those of Gosline. However, it is thought that Gosline's division Osteoglossi (of the Clupeiformes) should be raised to ordinal status. Two suborders are recognized, Osteoglossoidei and Notopteroidei, the latter divisible into the superfamilies Hiodontoidae and Notopteroidae (the detailed taxonomy of the Osteoglossoidei is not considered). A possible ancestry for the Osteoglossiformes is discussed.

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PLATE 1

Notopterus afer

Lateral view of swimbladder, showing the three major subdivisions :

A. Cranial and interconnecting portion ; B. Abdominal portion ; C. Caudal portion (posterior fifth not shown). In A are visible the elongate lateral auditory chamber followed by the two hemispherical chambers, and in B the subspherical sac with its posteriorly directed horn lying above the bilobed main abdominal chamber. The intrinsic superficial musculature has not been removed from the abdominal sac or the caudal part of the bladder. Some anal fin muscles have been dissected away to expose the ventral diverticula of the caudal swimbladder.

PLATE 1

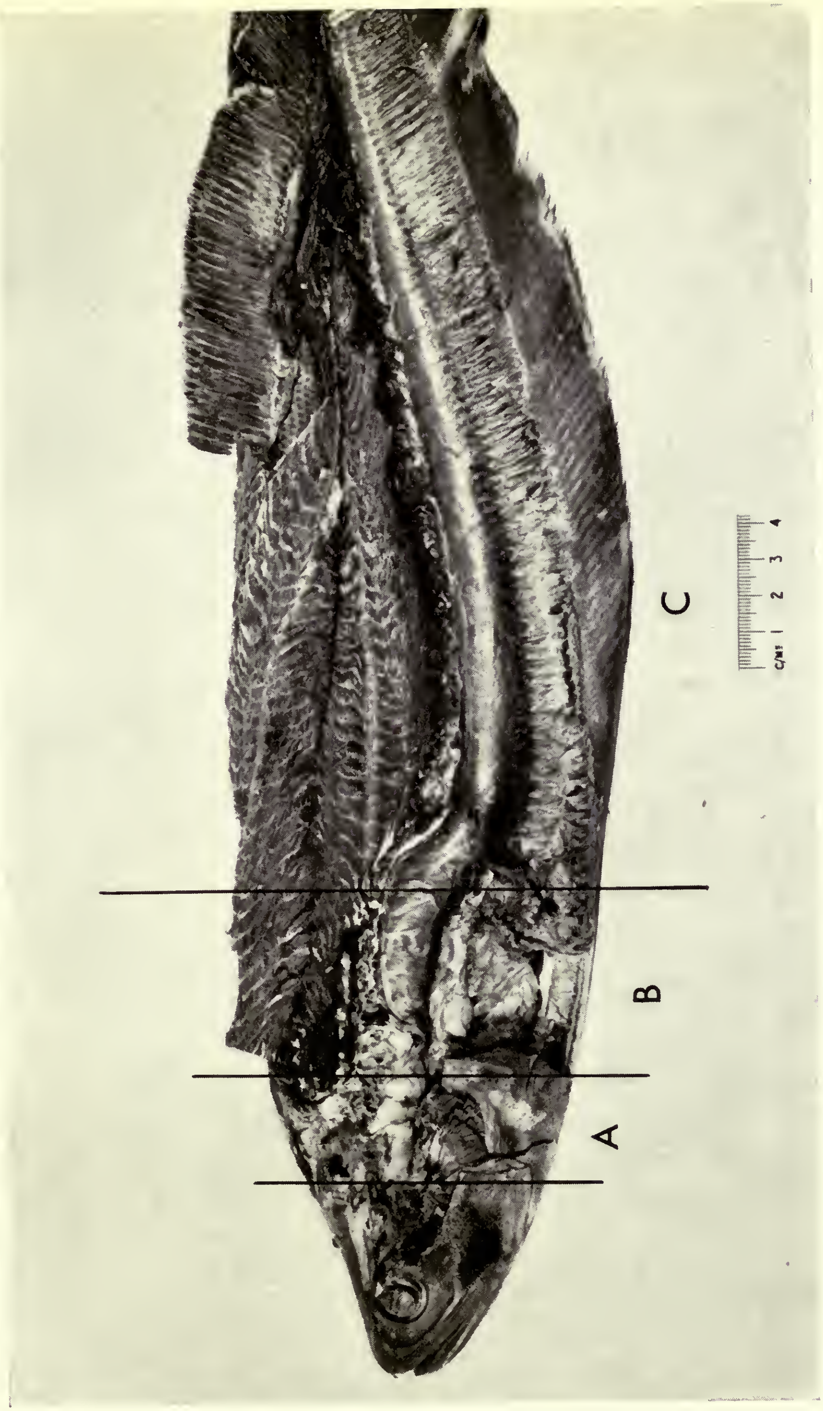
A
B
C
C/MS
1
2
3
4

PLATE 2

Notopterus afer

Enlarged left lateral view of cranial, interconnecting and anterior abdominal portions of the swimbladder. The wall of the dorsal horn is torn, as is the lower lateral aspect of the subspherical sac.

as : abdominal sac (bilobed portion) ; chs : contiguous hemispheres ; lac : lateral auditory chamber ; lhs : left horn developed from the subspherical sac ; ss : subspherical sac.

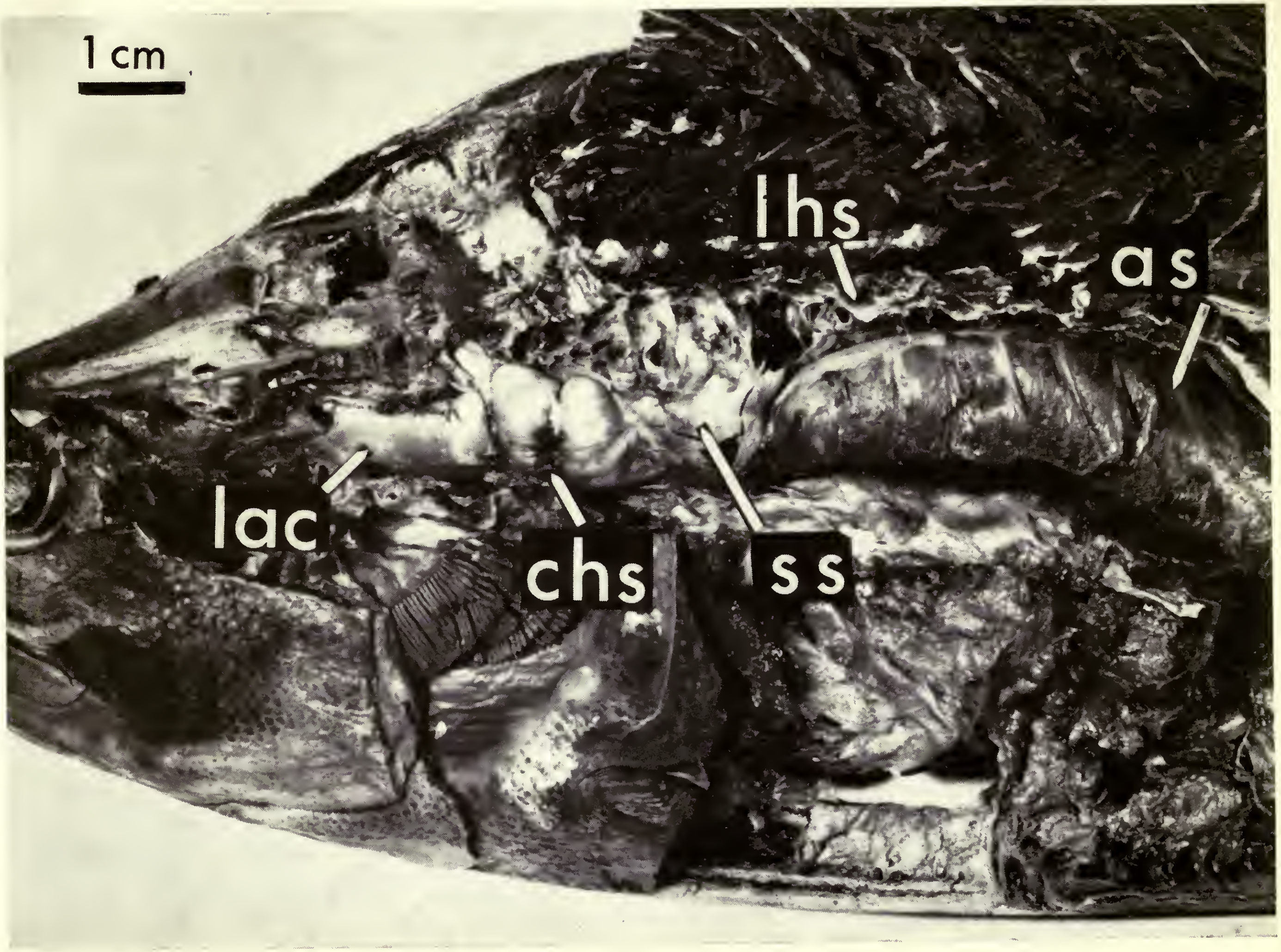
1 cm
lhs
as
lac
chs
ss

PLATE 3

Notopterus afer

Enlarged left lateral view of cranial, interconnecting and anterior abdominal portions after removal of the swimbladder wall.

csi : cavity lodging the left superior intracranial vesicle. (The medial wall of the right vesicle is visible at *.) ; e : epiglottis ; r : ridge marking boundary of the subspherical sac and the posterior member of the pair of contiguous hemispheres (chs. of Plate 2) ; tm : thickened margin of the lip surrounding the entrance to the common vestibule ; ts : oblique transverse septum separating the subspherical sac from the paired abdominal sacs.

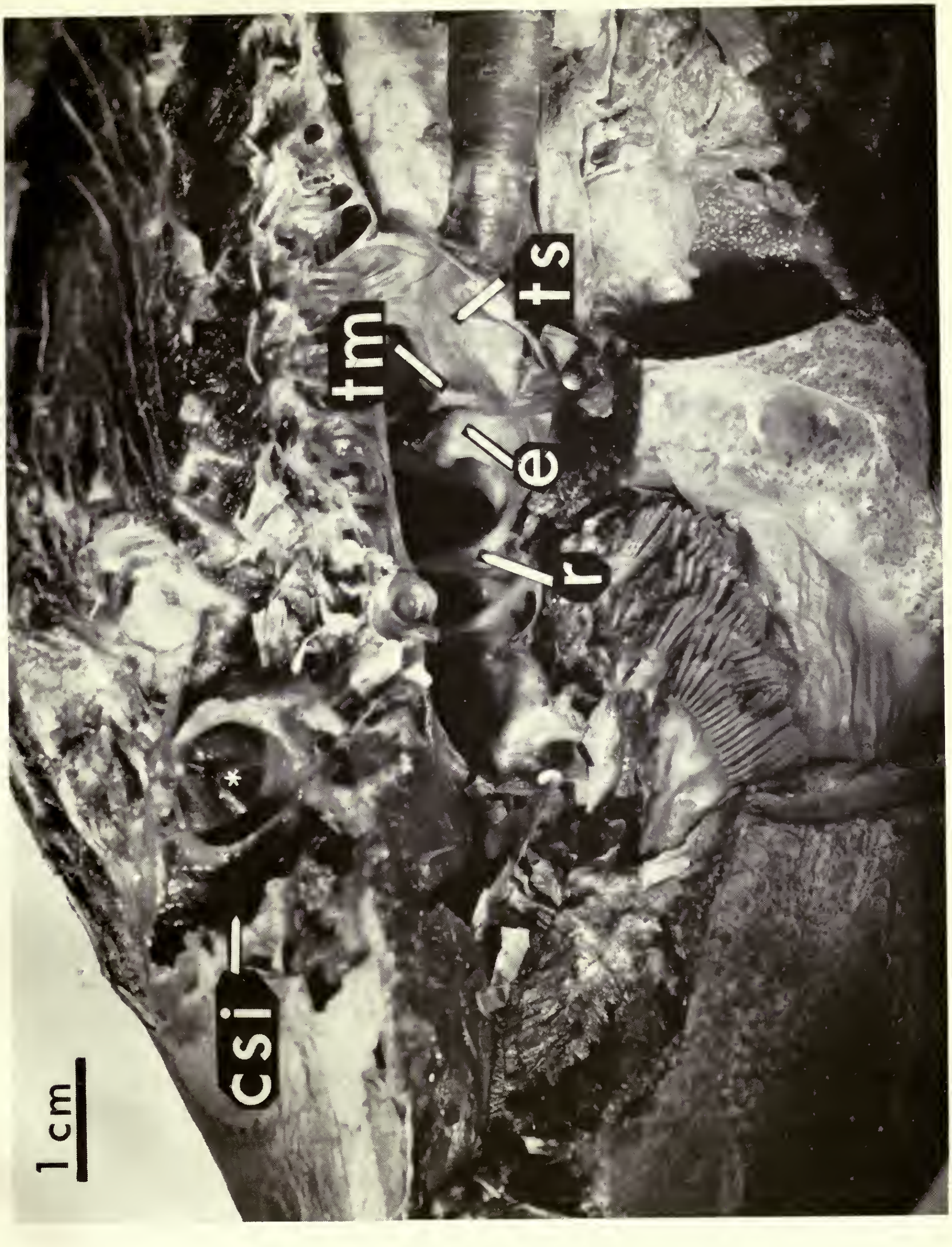
1 cm
csi
*
tm
ts
e
r

PLATE 4

Notopterus afer

Fig. 1. Entrance to the paired abdominal portion viewed from the right and somewhat ventrolaterally. The greater part of the lateral wall of the right-hand chamber has been cut away, and the common vestibule (together with the entrance to the right chamber) opened up. The epiglottis is in the erect position (*cf.* specimen figured in Plate 3).
e : epiglottis ; l : lumen of subspherical sac, with vertebrae showing through the thin *tunica interna ;* m.s : median septum separating the anterior portion of the left and right-hand chambers ; o : opening from common vestibule to left chamber.

Fig. 2. Oblique ventro-lateral view showing the dorsal wall of the right abdominal sac ; the alveoli are clearly visible.

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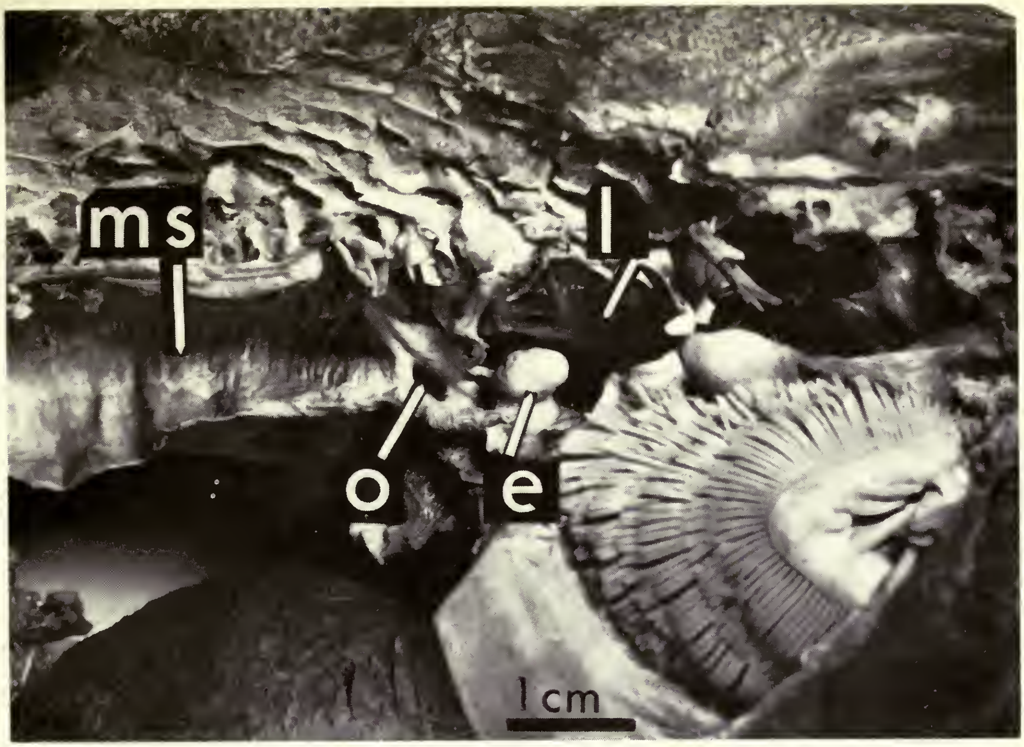

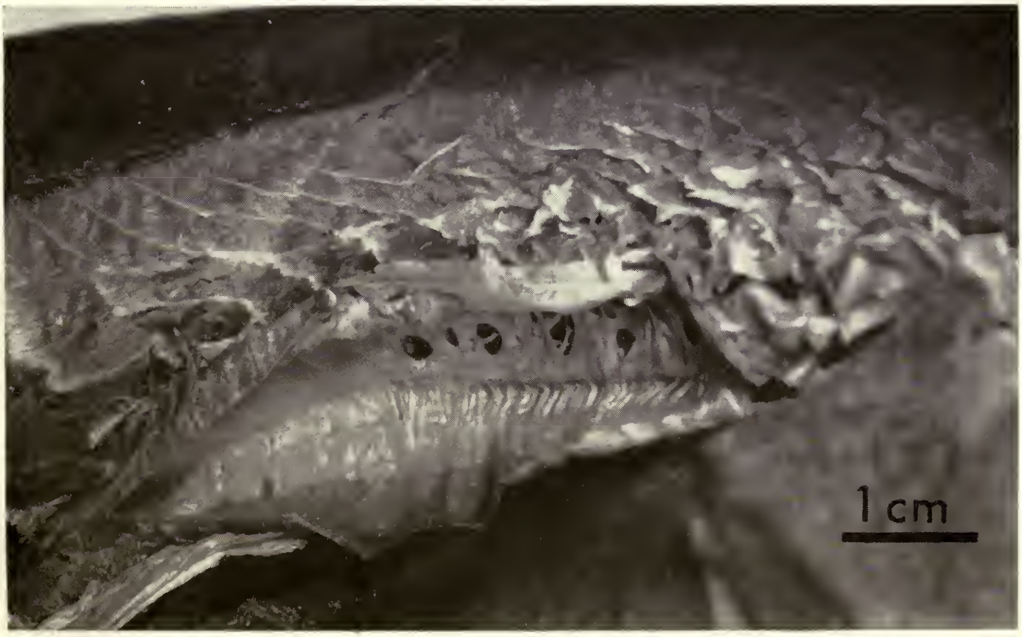

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A REVISION OF THE GENUS *ACARUS* L., 1758 (ACARIDAE, ACARINA)

D. A. GRIFFITHS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 11 No. 6
LONDON: 1964

6 APR

A REVISION OF THE GENUS *ACARUS* L., 1758 (ACARIDAE, ACARINA)

BY

D. A. GRIFFITHS

Agricultural Research Council, Pest Infestation Laboratory.
and
Royal Free Hospital School of Medicine, University of London.

Pp. 413–464 ; *Plate* 1 ; 43 *Text-figures*

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A REVISION OF THE GENUS
ACARUS L., 1758
(ACARIDAE, ACARINA)

By D. A. GRIFFITHS

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1. INTRODUCTION

Linnaeus (1758) included thirty-one species in his genus *Acarus*, most of which were mites. These species are now represented in four sub-orders of the Acarina and the genus is restricted so that only one of them, the "Flour mite", is included in *Acarus*.

This species, which is the most serious of all the mite pests of stored food products has been considered to be very variable, the variation indicating no more than racial differences. Two kinds of hypopi have been attributed to it and it has been recorded both in stored product and out-door habitats.

This paper summarises the taxonomic conclusions of a study made to test the hypothesis that these attributes possibly reflected differences between sibling species rather than racial variation within the " Flour mite ". Biological conclusions relating to hybridization between and hypopus formation within populations will be published elsewhere.

In the text, generic and specific headings are followed by a list of synonymies *sensu stricto*. A second list of abbreviated references is given at the end of certain specific descriptions ; these are classified as published descriptions or as misidentifications attributable to a particular species. Full bibliographic references for these synonymies *sensu lato* can be found in Appendix I which lists the names appearing in published descriptions considered during the course of this revision.

2. GENERIC CONSIDERATIONS OF *ACARUS* LINNAEUS, 1758

Acarus Linnaeus, 1758

Tyroglyphus Latreille, P. (1796). *Précis Caract. Ins.:* 185.

Aleurobius Canestrini, G. (1888). *Prospetto dell' Acarofauna Italiana,* **3** : 399–402, Tav 30, Fig. 1.

The name *Tyroglyphus* Latreille, 1796 has been placed on the Official Index of Rejected and Invalid Names in Zoology, as a junior objective synonym of *Acarus* L., 1758 (Hemming & Noakes, 1958a).

TYPE SPECIES : *Acarus siro* Linnaeus, C. (1758). *Syst. Nat.* (ed 10) **1** : 616 (as selected by Latreille, P. (1810). *Consid. gen. Anim. Crust. Arach. Ins.:* 425, 132 ; as interpreted by Fabricius, J. C. (1794). *Ent. Syst.* **4** : 430).

In 1758 Linnaeus recognised two varieties of *Acarus siro*, which he named *farinae* and *scabiei*. In his opinion they did not differ morphologically but had different habitats. His diagnosis for " *A. siro* " is given below, followed by his habitat records for the two varieties :

> " A. lateribus sublobatis pedibus quatuor posticis longissimis, femoribus capiteque ferrugineis, abdomine setoso."
>
> " Habitat in Farina Europae, Americae. Inter sirones Farinae, Scabiei, Dysenteria, Hemitritei, non reperi alias differentias, quam a loco petitas. Amoen. acad. **3**, p. 333."

In his personal copy of the tenth edition of *Systemae Naturae*, 1758 (now held by the Linnean Society, London) Linnaeus wrote above the words "in Farina Europae, Americae " the words " in caseo diutius asservatis ". This addition appears in print in the 12th edition of *Systemae Naturae*, published in 1767.

According to Declaration No. 94 of the International Commission on Zoological Nomenclature, *farinae, Acarus siro* [var.] Linn., 1758 is a junior objective synonym of *siro, Acarus* Linn. through the " First Reviser " interpretation made by Fabricius in 1794 ; this name *A. siro* Linn., as interpreted by Fabricius (1794), is the name of the type species of *Acarus* Linn., 1758 through the selection made by Latreille in 1810.

Fabricius' first account of *Acarus*, published in 1775, closely followed that of Linnaeus (1758). He, like Linnaeus, recognised a species *A. siro* with two varieties *farinae* and *scabiei*. However, in his second account of *Acarus*, published in 1781, among others he listed a species *A. siro* without varieties, followed by a species *A. scabiei*, also without varieties. His diagnosis and habitat locality for these two species is given below (I have inserted square brackets about certain words).

> " 21. *siro* A. [Albidus] femoribus capiteque ferrugineis, abdomine setoso."
>
> " Habitat in farinae. Caseo diutius asservatis."
>
> " 22. *scabiei* A. [Albidus], pedibus [rufescentibus] posticis quatuor [seta] longissimis."

> " Habitat in Ulceribus scabiei, cutem rugas secutus penetrat titillatiorem & vesiculam excitat. . ."

If we compare the above diagnosis with that previously quoted for " *A. siro* " L., 1758, the following observations can be made. Excluding those words which I have placed in parentheses, the two diagnoses of Fabricius (1781), when added together, constitute Linnaeus 1758 diagnosis for " *A. siro* ", except that Linnaeus' phrase " lateribus sublobatis " is omitted. The re-arrangement of Linnaeus' phrase " pedibus quatuor posticis longissimis ", together with the inclusion of the word " seta ", suggests that Fabricius believed this phrase referred to the " itch " mite, and that Linnaeus had mistaken the long terminal seta which arises from tarsus III and IV to be the terminal segment of leg III and IV. Oudemans (1913) independently reached the same conclusion.

A comparison of the habitat localities associated with these three descriptions reveal that the habitat of *A. siro* Fab. is identical to that of *A. siro* [var.] *farinae* Linn., as it appears in *Systemae Naturae*, edition 12 and the habitat of *A. scabiei* Fab. compares favourably with that of *A. siro* [var.] *scabiei* Linn., 1758.

In these circumstances we must conclude that, according to the " First Reviser ", Linnaeus had mistakenly compounded two species. Further evidence to support this conclusion is given by Heilsen (1946) who reported that Linnaeus was of the opinion that the varieties *farinae* and *scabiei* were identical as regards pathogenicity, and children might have scabies transmitted to them through being dusted with flour. I submit, therefore, that in his work of 1781 Fabricius, by recognising two species, was truly making a taxonomic advance. This work in spite of Declaration 94 thus truly constitutes the first revision. It follows that *farinae, A. siro* [var.] Linn., 1758 is objectively identical with *siro, Acarus* Linn., 1758, sensu Fabricius 1781.

Nomenclatorally, it is fortunate that Fabricius' 1781 and 1794 texts are virtually identical. In the 1781 text, but not in that of 1794, Fabricius gave a bibliographic reference to Schrank (1776), quoting in full the latter's description of the " Käsemilbe ". Schrank's 1776 description of this mite is illustrated by a figure which clearly shows the presence of an apophysis on the ventral surface of femur I.

Since there is only one generic entity known to science having this character amongst mites which have more than the remotest possibility of infesting flour and cheese, we can be sure which species or group of species Schrank (1776), Fabricius (1781) and Fabricius (1794) were considering. By Declaration 94, which informs us that Fabricius (1794) is the " First Reviser ", we therefore know with a high degree of certainty that *A. siro* [var.] *farinae* Linn., 1758 is a mite capable of infesting flour and cheese which has an apophysis on the ventral surface of femur I. Elsewhere in this paper I have shown that there are five validly described distinct species in this generic taxon. Two of these species are unlikely to be that considered by Schrank (1776) since he writes " setis corpore brevioribus " ; these two species (namely those referred to as *A. tyrophagoides* (Zachvatkin) and *A. gracilis* Hughes) have a " train " of setae extending from the posterior margin of the body. Moreover, both these species as far as we know are very rare, *A. gracilis* being confined to bat-roosts, *A. tyrophagoides* to forest litter in central Russia (see page 453). In the remaining three species, the body setae are very short. In this paper, these three species are collectively referred to as the *A. siro* complex.

It is not possible to recognise from their descriptions or figures which of the three species of the *A. siro* complex Linnaeus, Schrank or Fabricius were considering, since the micro-tarsal characters essential for their separation were of course not described by them. Can it be shown, that only populations of one of the three species of the complex are commonly associated with farinaceous products and with cheese? The answer is a qualified yes. Published records of the " flour mite " indicate a wide variety of habitats, namely, farinaceous products, cheese, harvested cereals, hay, grass, soil and the nests of animals and birds (see page 457 for references). This wide range of habitats stimulated a survey of material available to me (Appendix II and chapter IV). Its analysis shows that populations representing two of the three taxa making up the *A. siro* complex occur in out-door habitats ; they were not recorded from flour or other farinaceous products, but did occur on cheese. By comparison, populations representing the third taxon were recorded from flour six times and from farinaceous and other processed cereals on thirty separate occasions ; they also occurred on cheese, but were seldom found in out-door habitats. I conclude, therefore, that this last-mentioned taxon is *A. siro* [var.] *farinae* Linn., 1758. Because the three species of the *A. siro* complex do not have absolutely distinct habitats, and because no type material exists (see page 433), a neotype designation for *A. siro* [var.] *farinae* is made in this paper.

It is fortunate that the diagnosis of *Acarus* accepted today coincides essentially with that based on *A. siro* [var.] *farinae* as now interpreted. Recent generic revisions (Zachvatkin, 1941 ; Hughes, 1961) characterise *Acarus* upon structures which were first considered to have generic value by Canestrini (1888), although he referred to the taxon as *Aleurobius*. Canestrini made reference to Koch (1841) who was the first to report that the femoral apophysis was confined to the male of the species he called *Acarus farinae ;* neither referred to Schrank (1776) and Fabricius (1781 and 1794).

Generic Characters (*Adults*).

Setae v e less than half the length of v i. Solenidion sigma$_1$ (σ_1) on genu I more than three times length of sigma$_2$ (σ_2) on same segment. Setae d_1 and l a always short. First pair of legs of male enlarged, the femur of which bears a ventral apophysis (Text-fig. 1).

Distinguishing Characters (*Adults*).

Solenidia sigma$_1$ on genu I more than three times the length of sigma$_2$. Claws of female never bifid. Femur I of male enlarged, bearing ventrally a cone shaped apophysis.

Morphological Variation.

Many of the morphological characters of *Acarus* specimens show remarkably little variation from one individual to another and from species to species. Some are common to other genera within the family Acaridae whilst others serve to

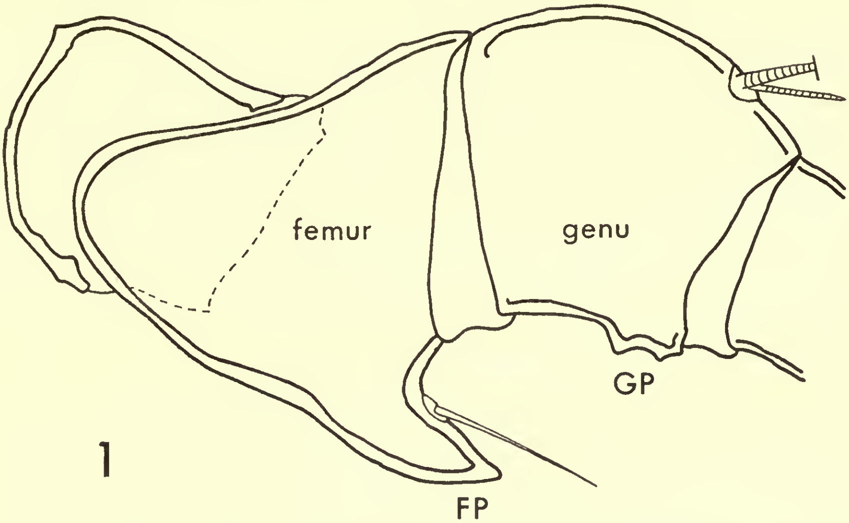


FIG. 1. *Acarus siro* L., male. Femur I and genu I, illustrating femoral apophysis (FA) and genual protrusions (GP). ×2100.

distinguish the genus *Acarus*. These characters are discussed below with reference to the adult stage.

The number of pairs of setae on the dorsal and ventral surfaces of the body is constant. I have never found an individual in which a pair or one of a pair of setae is suppressed. The position of these setae is the same for all species except that in *A. gracilis* specimens setae d_2 are much closer to setae d_1. The length of the vertical internal setae is always about 4 to 5 times that of the vertical external setae.

The structure of the male or female genitalia is extremely similar for all species. Robertson (1961) in her study on variation in the closely related genus *Tyrophagus* found specific differences in the morphology of the male genitalia. I have not found this to be the case in the genus *Acarus* ; the species cannot be separated on the shape of the penis or its supporting structures.

The male secondary sexual characters are common to all species. In only one case can they be used to differentiate a species and this provides a separation between *A. gracilis* and the *A. siro* complex. In *A. gracilis* the pair of suckers on tarsus IV are large and close together on the basal third of the tarsus whereas in specimens of the *A. siro* complex they are much smaller and separated by a greater distance.

Morphological characters which serve to differentiate the species are given in the key to species. These do, of course, vary between specimens but the amount of overlap between species is either extremely small and probably due to imperfections in mounting technique or non-existent. Only one of the diagnostic characters can, by itself, be used to distinguish between all the species in the genus. This character is solenidion omega$_1$, situated on tarsus I and II (Plate 1). Because the difference is one of shape, orientation of the specimen plays an essential part when the identity of a specimen rests solely on this character. In the closely related genus *Tyrophagus*

Ouds., 1924, the shape of solenidion omega$_1$ is different for many species (Hughes, A. M., 1961 ; Robertson, 1959).

Griffiths (1963, Ph.D. thesis unpub.) has shown that characters which Oudemans used in 1905 and 1913 to distinguish the species *Acarus farris* (Ouds. 1905) are not reliable. He also suggests that the variation exhibited by these characters is probably diet-related or due to variation in angle of viewing. The characters which Oudemans selected are:—

1. Intensity of colouring of the appendages ;
2. The number of pectinations on the supra-coxal seta ;
3. The number of protrusions of Grandjean's organ ;
4. Length and shape of tarsi ;
5. Relative length of idiosomal setae.

3. KEYS TO AND DESCRIPTIONS OF SPECIES

Key to Adults

1 Dorsal setae d$_2$ and d$_3$ not more than twice the length of d$_1$ . . (***A. siro*** complex) 2

– Dorsal setae d$_2$ or d$_3$ five to six times longer than d$_1$ 4

2 Ventral, distal spine " s " of tarsi I and II (not tarsus I of ♂) large, about equal to length of tarsal claw ; ventro-posterior margin concave, tip directed backwards (Text-fig. 18). Solenidion omega$_1$(ω_1)[1] of tarsus II recumbent, with distinct " goose-neck " before terminal expansion (Pl. I, fig. 1) . . . ***A. siro*** (p. 432)

– Spine " s " slender, about half length of tarsal claw ; ventro-posterior margin convex, tip directed forward (Text-figs. 6 & 24). Solenidion omega$_1$ at 45° angle, without distinct neck preceding terminal expansion 3

3 Omega$_1$ with sides expanding gradually from base then narrowing to an indistinct neck before expanding into terminal head. Width of widest part of head equal to width of widest part of stem (Pl. I, fig. 2) . . . . ***A. farris*** (p. 421)

– Omega$_1$ with sides almost parallel, expanding into a distinct egg-shaped terminal head which at widest part is wider than widest part of stem (Pl. I, fig. 4) ***A. immobilis*** sp. n. (p. 443)

4 Scapular setae (sc e and sc i) of almost equal length ; d$_2$ five to six times longer than d$_1$ (Text-fig. 34). Omega$_1$ of tarsus I and II gradually tapering from base to apex (Pl. I, fig. 3) . . . . ***A. gracilis*** (p. 448)

– External scapulars (sc e) more than twice length of internals (sc i) ; d$_2$ about equal in length to d$_1$, with d$_3$ five to six times longer (Text-fig. 40). Omega$_1$ gradually expanding from base to apex (Text-fig. 41) . . . ***A. tyrophagoides*** (p. 453)

Key to hypopi

1 In dorso-ventral mount, terminal three or more segments of legs I and II extend beyond margin of body. Gnathosoma bears pair of long terminal aristiform bristles. Sucker plate with eight distinct suckers . . (Motile hypopal form) 2

– Legs short ; in dorso-ventral mounts tarsi of legs I and II are the only segments completely visible. Gnathosoma rudimentary, aristiform bristles not present. Only one pair of well-developed suckers on sucker plate . (Inert hypopal form) 3

2 Hysterosomal setae d$_1$, d$_2$, d$_3$ and l$_1$ almost as long as scapulars (sc i and sc e). Sc i about 1·2 times length of d$_1$ and 1·5 times l$_1$. Setae d$_1$ and l$_1$ about 3 times longer than d$_4$ (Text-fig. 16). Bases of genital setae and flanking pair of coxal suckers almost in line, distance between base of sucker and base of seta is less than width of setal base (Text-fig. 17) . . . . ***A. siro*** (p. 434)

---

[1] All descriptions of solenidion omega$_1$ are based on true lateral views.

– Hysterosomal setae appreciably shorter than scapulars. Sc i about 2 times length of d_1 and 3 times l_1. Setae d_1 and l_1 about equal in length to d_4. Bases of genital setae just forward of coxal sucker bases. Distance between base of sucker and base of seta about equal to width of setal base (Text-fig. 5) . ***A. farris*** (p. 425)

3 On sucker plate the central pair of suckers vestigial, anterior peripheral pair moderately well developed (Text-fig. 27). All setae on tarsus III and IV shorter than length of tarsus, spine-like, never leaf-shaped (Text-figs. 30 and 31). Omega$_1$ long, at least twice length of tarsal claw (Text-fig. 28) . . . ***A. immobilis*** (p. 445)

– Central pair of suckers are well developed, peripheral pairs vestigial (Text-fig. 35). All setae on tarsus III and IV longer than length of tarsus, leaf-like or pectinate (Text-figs. 38 and 39). Omega$_1$ at least three times shorter than tarsal claw (Text-fig. 36) . . . . ***A. gracilis*** (p. 450)

The *Acarus siro* complex

This includes three species which have been confused one with another and generally referred to under the name *Acarus siro* L., 1758 or *Tyroglyphus farinae* Latreille or *Aleurobius farinae* of various authors. A new specific name is proposed for one of the species which has not been recognised as distinct and for which no valid name is available. *Acarus farris* (Oudemans, 1905) is re-erected and included in the complex and the third species is *Acarus siro* L., 1758 for which a neotype is designated. An appendix to this paper lists the names appearing in published descriptions which have been considered.

In this paper, differentiation of the species making up the complex is based on morphological differences in the adult and hypopal stages. Griffiths (1962) and (1964 in prep.) has established, through hybridization experiments, that the species are reproductively isolated, although some gene exchange between species is possible.

Acarus farris (Oudemans, 1905) **comb. n.**

Aleurobius farris Oudemans, A. C. (1905). *Ent. Ber. Amst.* **2** (26) : 20.

In 1913 Oudemans described *farris* more fully and transferred it to the genus *Tyroglyphus*. In 1925 he reduced *farris* to below species level saying that it could, at the most, be regarded as a weak race of *Tyroglyphus farinae* L.

SYNTYPES : in Oudemans' collection there are seven slides of this species labelled " Type ". They represent material taken from three separate localities at different times. Since Oudemans' original description is based on the material from one of the three localities, then only specimens making up this material are syntypes, namely ; specimens on slides numbered 45, 46 and 47 ; taken from cheese, Arnhem, February 1902. From these specimens I have previously selected as lectotype the single male mounted on slide number 45 (Griffiths, 1962). Other specimens seen are listed under " habitat and distribution records " (see page 431).

MALE (Text-fig. 2). Length of idiosoma of six males, reared on wheat germ at 90 per cent relative humidity and 20°C., = 0·365 mm. average.

Idiosomal measurements were taken from the centre of an imaginary line connecting anterior tips of the epimeron fork to the centre of the posterior margin of the body.

The body is colourless, the legs and part of the gnathosoma vary in colour according to the diet. The limbs of mites collected from out-door habitats are generally pale yellow or pale rose, whereas culture reared mites feeding on yeast or wheat germ have dark red to reddish brown legs and gnathosomal extremities. Mites reared on gluten resemble wild populations in their colouring.

The body is oval, the posterior margin is evenly rounded.

(i) Body setae :

These are fine, some are smooth and others sparsely pectinate. On the dorsal surface the following pairs of setae bear pectinations which are easily visible when viewed with an oil immersion objective of phase-contrast equipment:

vertical internals (v i)
both pairs of scapulars (sc e) and (sc i)
internal sacrals (sa i)

Pectinations of the following pairs of setae are spaced further apart and are less distinct :

external verticals (v e)
external humerals (h e)
posterior laterals (l p)
fourth dorsals (d_4)
external sacrals (sa e)

The following pairs of setae appear to be smooth :

first dorsals (d_1)
second dorsals (d_2)
third dorsals (d_3)
internal humerals (h i)
anterior laterals (l a)

With the exception of the ventral humeral pair of setae (h v) all setae on the ventral surface are devoid of pectinations. This includes the long, stout pair of posterior anal setae (pa_2).

(ii) Dorsal surface :

A propodosomal dorsal shield is present. The shield is roughly bell shaped, its anterior corners are acute and the posterior corners well rounded. It extends from the bases of the v i setae (which are just within and central of its anterior border) to a point just in front of setae sc i.

The v i setae extend forward over the gnathosoma. In life, they diverge slightly outwards and curve downwards over the chelicerae. The v e's are one fifth as long as v i's and arise contiguous with the lateral margins of the propodosomal shield, close to the anterior corners. Two pairs of scapular setae (sc e and sc i) arise in a transverse row across the propodosoma, behind the shield and on a level with coxae II. Sc e are a little longer than sc i. Expressed as a percentage of the idiosomal measurement used here they are 23·5 and 23·0 per cent, respectively.

A pair of Grandjean's organs arise from the anterior-lateral margins of the propodosoma. Each is a flattened semi-circular plate, the free margins of which are drawn out into flame-like filaments. The plate is partially cleft down the centre, dividing the filaments into two groups. A few of the processes nearest to the cleft are quite long and appear to follow a similar pattern in all specimens. The filaments on the lateral edges of the plate are small and numerous. Because this organ is difficult to perceive and appears to vary in shape, possibly according to the angle of viewing, it is not used as a diagnostic character in this work. A lateral sclerite curves backwards from the base of each Grandjean's organ, encircling above coxa I. A supra-coxal seta arises from the posterior part of each sclerite. This seta is expanded at the base, tapering to a fine slender point. Strong pectinations branch out along its entire length.

The normal complement of setae for the Acaridae arise from the dorsal surface of the hysterosoma. Their position relative to one another is given in Text-fig. 2. Sa i is the longest, at about thirty-six per cent. of the idiosomal length. The remainder are quite short with average lengths as follows ; d_1 – 5%, d_2 – 7·5%, d_3 – 8·7%, d_4 – 9·5%, l a – 5%, l p – 10%, sa e 9·3% of idiosomal length.

Three pairs of circular " pores " (function unknown) are situated on the dorsal surface of the hysterosoma. One pair arise just behind the h e setae ; another on the lateral margins of the body just anterior to the openings to the " fat " or latero-abdominal glands, which themselves open on to the surface a little behind and dorsal of coxa IV. The third pair lie on the postero-lateral border of the body, just lateral to the bases of sc e (Text-fig. 2.)

(iii) Ventral surface :

A pair of ventral humeral setae (h v) lie immediately in front of coxae II ; two pairs of coxal setae just forward of coxa I and IV ; three pairs of genital setae (g) and one pair of anal setae (pr a), one on each side of the anterior half of the anal opening which is a slit-like opening on mid-line of body. All these setae are short, never longer than l p ; h v are pectinate, the remainder smooth with whip-like extremities. Posterior half of the anal opening is straddled by a pair of anal suckers. The bases of six setae (three pairs of post anals pa) form an arc which runs parallel to hind margin of the body. The most anterior pair (pa_1), one at each end of the arc, arise well behind the posterior margins of the anal suckers ; they are short, barely reaching the edge of the body. The second pair (pa_2) are three times longer and the third pair (pa_3), in line with and posterior to the anal suckers, are about twice as long as pa_1 ; all these setae are smooth. A pair of circular pores are lateral and external to pa_3.

The genital aperture, in mid-line between coxae IV, is large ; lateral arms of penis support slender, diverging posteriorly with slightly incurved tips. Basal element of penis with curved posterior margin, extremities enlarged. Penis is a short truncated tube curved downwards at apex.

Apodemes of legs I united in mid-line forming a short sternum ; those of legs II, III and IV free. Apodeme III narrow along entire length ; those of legs II and IV with distal half expanded to broad paddle-shape, each terminating in short backward directed hook.

(iv) Legs :

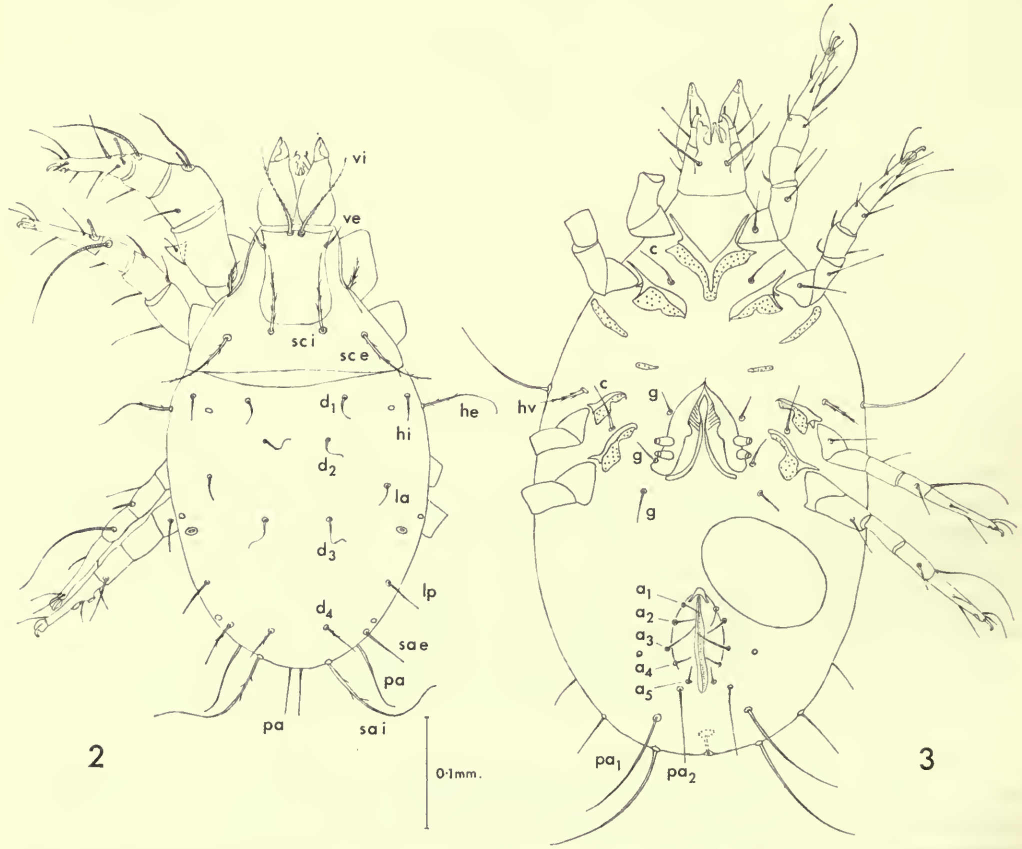
Five segmented with a well-developed pre-tarsus terminating in stalked claw.

Genu and femur leg I much enlarged ; strong spur or apophysis projecting downwards and forward from ventral surface of femur ; femoral seta (vF) arises from base of spur ; ventral surface of genu bearing two small tooth-like projections. Tarsus IV bears two copulatory suckers.

FEMALE (Text-fig. 3). Body larger and more roundly oval. On dorsum, the idiosomal setal pattern and pectinations, Grandjean's organs, supra-coxal setae, propodosomal shield and circular " pores " are as for male.

(i) Ventral surface :

Differs from male in absence of anal suckers, structure of genital aperture and number plus arrangement of anal and post-anal setae.



FIGS. 2–3. Fig. 2, *Acarus farris* (Ouds.) ♂. Dorsal view. Setae of the idiosoma : ve, vi, sc e, sc i, he, hi, d_1 to d_4, la, lp, sa e, sa i. Fig. 3, *Acarus farris* (Ouds.) ♀. Ventral view. Setae of the idiosoma : hv, c, g, a_1 to a_5, pa_1, pa_2.

Genital aperture (Text-fig. 3) is an elongate slit along mid-line of body, extends from coxa III back to coxa IV and is enclosed by two diverging genital folds which are also present in male. Anal opening (Text-fig. 3) surrounded by five pairs of anal setae (a_1 to a_5) ; a_1, a_4 and a_5 about equal in length ; a_2 about one third longer and

a_3 about twice as long. Only two pairs of post anal setae present (pa_1 and pa_2) ; pa_2 about twice length of a_3 and barely reaching posterior margin of body ; pa_1 about twice length of pa_1, extend well beyond posterior margin of body. In centre of this margin bursa copulatrix opens into base of a cuticularised saucer-shaped structure.

(ii) Legs :

Legs I not wider than others ; femur I not bearing spur and genu I without projections ; tarsus IV not bearing copulatory suckers.

LARVA. Setae, in proportion to idiosomal length, shorter than those of adult ; sc's shorter than v i ; pa twenty per cent of idiosoma. Pair of coxal rods on coxal fields I, elongate cylinders terminating in a transparent sphere. Setae d_4, two pairs genitals, anals and two pairs of post anals absent ; no genital sensory organs. Three pairs of legs.

PROTONYMPH. Dorsal setal pattern as for adult but proportionally shorter ; d_4 present. Ventral surface differs from larva and adult in that one pair of genital setae, three pairs anal, one pair post anal setae and one pair genital sensory organs are present. Coxal rods absent. Four pairs of legs present.

TRITONYMPH. Very like adult female, except that setae are a little shorter and genital aperture is present as a single slit-like opening not enclosed by folds.

HYPOPUS (Text-figs. 4, 5). This is a motile form.

Body length (anterior margin of propodosoma to posterior margin of hysterosoma): average 20 specimens = 0.240 mm.

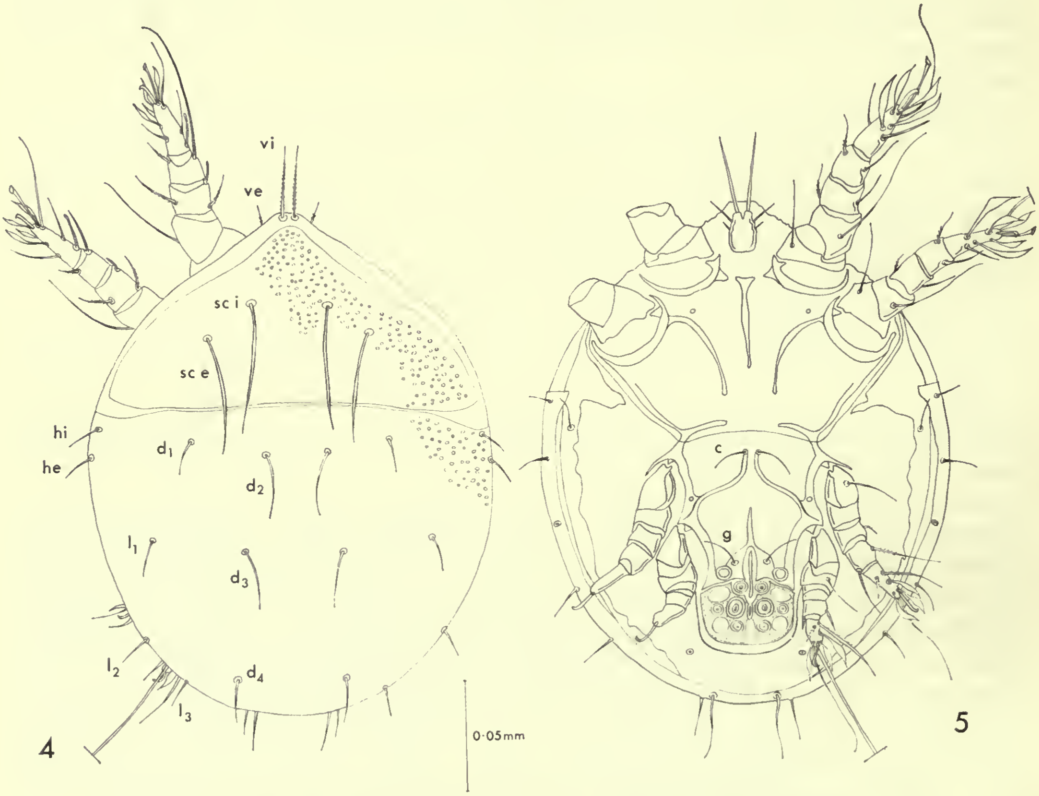
Colour of live specimens pinkish-beige. Dorsal surface, convex with fine irregularly spaced punctations, is divided into a distinct propodosoma and hysterosoma. Eyes not present.

Strongly pectinate v i setae project forward from tip of propodosoma. They are about ten per cent of body length ; v e are one fifth as long. Bases of two pairs scapular setae traverse propodosoma on level with coxae II ; both pairs are fairly long about twenty five per cent of body length, sc i being slightly longer than sc e.

Setae of hysterosoma appreciably shorter than sc i and sc e. Four pairs arise in a transverse row immediately behind groove which separates propodosoma from hysterosoma ; h e and h i near latero-anterior margin of hysterosoma and d_1, d_2 with bases in line with bases of scapulars. Thus, pair d_2 is displaced forward compared with its position in the adult and other stages. Pairs d_3 and d_4 are in linear series with d_2. Seta d_1 is slightly longer than d_4 ; d_2 and d_3 are about 1·5 times d_1. Three pairs of short laterals present ; l_1 is lateral to d_3, almost same length as d_1 and a little shorter than d_4; l_2 and l_3 lie on body margin between l_1 and d_4. Two pairs of setae, possibly homologous with the sacrals, project from posterior margin of body. A pair of glands open on lateral margin of body on a level with coxae IV.

On the ventral surface the gnathosoma is a much reduced unpaired plate, terminating in a pair of lobes from each of which an aristiform bristle arises. Two pairs of shorter bristles occur on lateral margins of plate. No mouth.

Sternum not forked, free as are apodemes I. Epimerites II well marked, extending backwards and converging slightly to join apodemes III, then running forwards and inwards towards mid-line of body. Apodemes IV curve gently forwards towards mid-line but just before meeting they angle sharply forward, running parallel on either side of mid-line for a short distance before ending ; not meeting apodemes III. A pair of coxal setae arise on surface of body at point where apodemes IV peter out. Rims of coxal cavities II, III and IV distinctly thickened. Internal rims of coxae IV " L " shaped, horizontal arms running parallel to anterior margin of sucker plate, then forward on either side of genital opening, fusing anteriorly to genital opening and then proceeding forward for short distance along mid-line.



FIGS. 4–5. *Acarus farris* (Ouds.), hypopus. Fig. 4, dorsum. Fig. 5, venter.

A pair of genital setae arise on either side of genital slit ; laterally, and at forty-five degrees backward from each seta, is a sucker ; the distance between bases of sucker and seta is about the width of the setal base.

Sucker plate (Text-fig. 5) small, consisting of central pair large suckers surrounded by three pairs of peripherals ; anterior pair shaped like a truncated cone, projecting further from body than the others. Four clear areas, which Hughes (1961) considers to be vestigial suckers, separate the three pairs of peripheral suckers.

LEG CHAETOTAXY OF ALL STAGES. The nomenclature used is that devised by Grandjean (1939).

(i) Female (Text-figs. 6, 7 and 8), male (Text-fig. 9) and tritonymph.

Leg I of these three stages bears the most solenidia and setae ; legs II, III and IV show progressive simplification (see formulae below). Chaetotaxy of tritonymph legs identical to that for corresponding legs of female, as are legs II and III of male ; certain modifications occur on tarsi I and IV of male.

Distal end of tarsus I encircled by eight setae ; d, e, f, fine slender smooth, p, q, u, v and s are short spines. Seta d, situated dorsally, is the longest ; f on post-axial face is half the length of d ; e on pre-axial face short, half length of f. Ventrally,the pair of spines v and u lie on either side of mid-line anterior and internal to pair p and q ; all four spines are small, slender and difficult to see. Spine s lies on mid-line posterior to others ; when viewed laterally, spine s is about half to two thirds length of tarsal claw.

Solenidion omega$_3$ (ω_3) is anterior to d just post-axial to mid-line. Mid region of tarsus bears whorl of four setae, ba, la, ra and wa. Basal third bears two solenidia, omega$_1$ (ω_1) and omega$_2$ (ω_2), the famulus, epsilon (ε), and one seta aa. Omega$_1$, when viewed laterally, has margins which diverge slightly from base upwards then narrow almost imperceptibly before expanding slightly into a terminal head ; the angle between its anterior margin and dorsal surface of tarsus is rarely less than forty-five degrees.[1] See Pl. I, fig. 2.

Famulus, (ε) shaped like a minute spine, arises from a small pit anterior to omega$_1$. Omega$_2$ rod-shaped half length of omega$_1$, situated on post-axial face.

Setae of tibia I (gT and hT) strongly pectinate ; solenidion psi (φ) long, whip-like, arising from distal dorsal point of tibia and extending beyond extremity of tarsus.

Genu I setae (cG and mG) also strongly pectinate. Two solenidia, sigma$_1$ (σ_1) and sigma$_2$ (σ_2), project from a depression on dorsal distal margin of genu ; sigma$_1$ about three times longer than sigma$_2$. Femur I and trochanter I each bear a single seta, vF and pR, respectively. Chaetotaxy of leg I of male same except spines v and u are fused forming a single scale-like spine larger than s, which is a thin spine.

Leg II as for leg I except aa, omega$_2$, omega$_3$ and one sigma are absent (Text-fig 7). Leg II of male same.

On leg III, setae ba, aa, l, gT, cG, wF are missing ; kT, nG and sR present and homologous with hT, mG and pR, respectively. Only two solenidia present, psi and one sigma (Text-fig. 8). Leg III of male same.

Psi is the only solenidion on leg IV. Setal pattern differs from leg III in that nG and sR are absent but wF (homologous with vF) is present. In the male, setae d and e of leg IV are modified into copulatory suckers (Text-fig. 9).

(ii) Protonymph and larva.

Chaetotaxy of protonymph and larva show progressive simplification, especially of solenidia. The number of setae and solenidia per segment of each leg is given below in formula fashion. Omega$_1$ of tarsus I and II in these stages has a much more defined expansion at distal end than that of adult.

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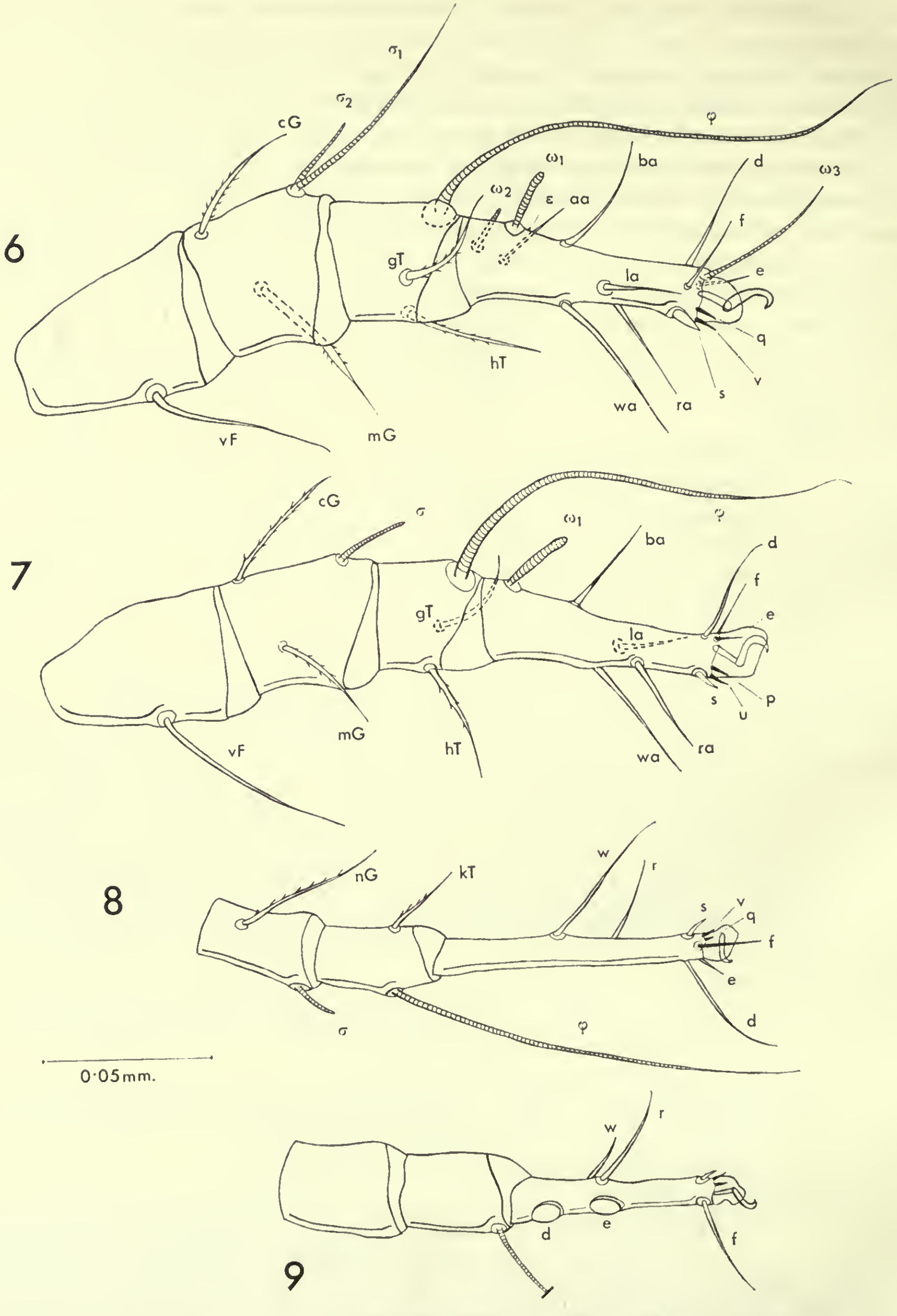
[1] In the male and female, omega$_1$ of tarsus II is slightly longer than that of tarsus I. In the tritonymph, on both tarsus I and II it is more distinctly expanded at the distal end.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FIGS. 6–9. *Acarus farris* (Ouds.), adult leg chaetotaxy. Fig. 6, leg I ♀—tarsus, tibia, genu, femur. Fig. 7, leg II ♀—tarsus, tibia, genu, femur. Fig. 8, leg III ♀—tarsus, tibia, genu. Fig. 9, leg IV ♂—tarsus, tibia, genu.

(iii) Hypopus (Text-figs. 10, 11, 12 & 13).

Adapted as it is to a special mode of life, the chaetotaxy of the hypopus is different from that of the other stages. Most of the differences involve a change in shape, but a few are concerned with the expression or suppression of certain setae and solenidia. The differences are dealt with under various sub-headings, below :

(a) Structures suppressed in hypopus but present in protonymph, tritonymph and adult stages.
Omega$_2$ and one sigma on leg I, and a sigma on leg III.

(b) Present in hypopus absent in all other stages.
Seta l on legs III and IV.

(c) Arises for first time in hypopus stage.
Seta pR on legs I and II ; seta sR on leg III ; on leg IV setae e, f, kT, wF and a very short solenidion psi.

(d) Fusion of ventral spine complex in hypopus stage.
Ventral spine complex of other stages replaced by two expanded leaf-like setae.

(e) Difference in shape or in length of solenidia and setae.
The length of omega$_1$ on tarsus I and II is just over half the length of the tarsus ; it is also much more slender than that of other stages.
Setae e, f, ra, r, la, l, wa and w are different in shape. On tarsus I and II seta e is expanded at the distal end into a sucker-like structure, on tarsus III it is leaf-like and on tarsus IV it is an extremely long, thick, simple seta, about half the length of the idiosoma. Seta f is thin, transparent and leaf-like on all legs ; ra or r is leaf-like on all legs except IV where it is simple ; la or l is long and leaf-shaped on all four legs ; wa is broad, flattened and heavily pectinate ; w is broad, flattened and smooth. Solenidion psi of tibia III is of medium length and does not taper to a whip-lash.

(iv) Chaetotactic formulae.

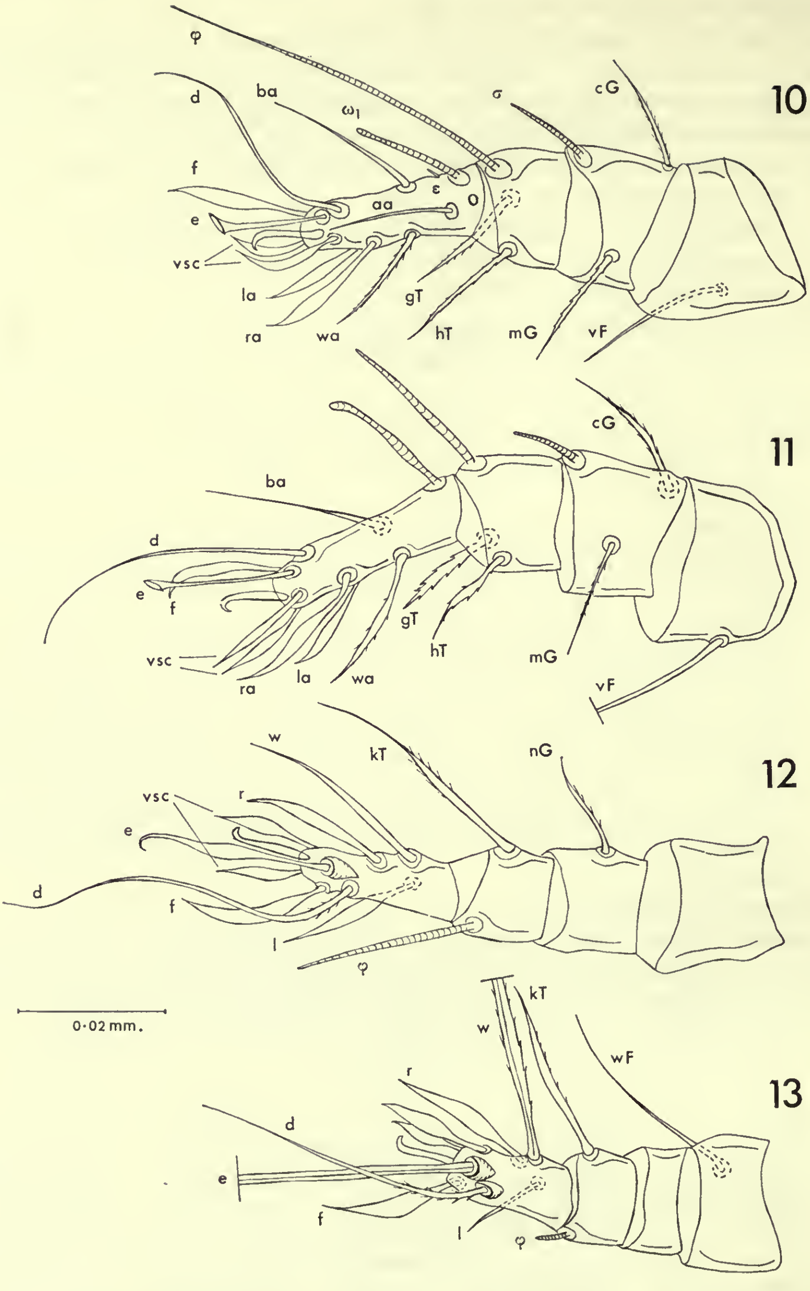
The numbers of setae and solenidia on each segment of each leg of all stages is given below in formula fashion. The famulus, which is present on tarsus I of all five stages, is not included. The five groups of figures inside each pair of brackets represent, from left to right ; tarsus, tibia, genu, femur and trochanter.

(*a*) SETAE

	Leg I	II	III	IV
Larva	(13.2.2.1.0)	(12.2.2.1.0)	(10.1.1.0.0)	(—)
Protonymph	(13.2.2.1.0)	(12.2.2.1.0)	(10.1.1.0.0)	(7.0.0.0.0)
Hypopus	(10.2.2.1.1)	(9.2.2.1.1)	(8.1.1.0.1)	(8.1.0.1.0)
Tritonymph	(13.2.2.1.1)	(12.2.2.1.1)	(10.1.1.0.1)	(10.1.0.1.0)
Adult	(13.2.2.1.1)	(12.2.2.1.1)	(10.1.1.0.1)	(10.1.0.1.0)

(*b*) SOLENIDIA

	Leg I	II	III	IV
Larva	(1.1.2.0.0)	(1.1.1.0.0)	(0.1.1.0.0)	(—)
Protonymph	(2.1.2.0.0)	(1.1.1.0.0)	(0.1.1.0.0)	(0.0.0.0.0)
Hypopus	(1.1.1.0.0)	(1.1.1.0.0)	(0.1.0.0.0)	(0.1.0.0.0)
Tritonymph	(3.1.2.0.0)	(1.1.1.0.0)	(0.1.1.0.0)	(0.1.0.0.0)
Adult	(3.1.2.0.0)	(1.1.1.0.0)	(0.1.1.0.0)	(0.1.0.0.0)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FIGS. 10–13. *Acarus farris* (Ouds.), hypopal leg chaetotaxy (excluding trochanter segment). Fig. 10, left leg I. Fig. 11, left leg II. Fig. 12, left leg III. Fig. 13, left leg IV.

Distribution. England, Scotland, Wales, Netherlands, Germany, Kenya, U.S.A. (possibly France, Morocco, Bermuda).

Habitat and Locality.

(i) A. C. Oudemans' collection, Leiden :

Utrecht (habitat not given), Sept. 1885 ; on cheese, Arnhem, 6.ii.1902 ; on cheese, Bremen, 16.ix.1904 ; on cheese, Leiden (date not given) ; *Mus rattus* (hypopus only), Arnhem, 8.x.1904 ; *Mus decumanus*, Arnhem, March 1909 ; *Cavia cobdya*, Arnhem, Feb., 1909 ; in insect collection (hypopus only), Amsterdam, 1916 ; in hole in an apple, Arnhem, 17.iii.1918 ; Berlin (habitat not given) (hypopus only), 14.v.1923 ; on the flower beetle *Osmoderma eremita* (hypopus only), Weenen, Aug., 1924 ; on a hyacinth bulb, Sassenheim, Feb., 1924.

(ii) D. A. Griffiths' collection :

At base of old barley stack in field (including hypopus), Abingdon, Wilts, July, 1959 ; in garden humus (including hypopus), Slough, Bucks., Aug., 1959 ; in hay in stables (hypopus only), Gloucestershire, Sept., 1960 ; in deep litter of chicken house (including hypopus), Hull, E. Yorks., Oct., 1960 ; in H.G. oats in farm granary (including hypopus), Haverfordwest, Pembs., Nov., 1960 ; in H.G. barley, Soulbury, Bucks., Dec., 1960 ; in sparrow's nest (including hypopus), nesting box no. 3, Kinloch farm, Island of Rhum, Scotland, Nov., 1960 ; in H.G. oats from Isle of Man, on M.V. Rema, Plymouth, June, 1961.

In farm granary (including hypopus), Kinangop, Kenya, March, 1962.

(iii) Pest Infestation Lab. (Slough) collection :

In H.G. barley (including hypopus), Scotland, May, 1945 ; on Cynipid in H.G. wheat (hypopus only), Newport, Mon., June, 1945 ; H.G. wheat (incl. hypopus), Sutton Bonington, Leics., Sept., 1945 ; grain store (incl. hypopus), Slough, Bucks., June, 1947 ; on Stilton cheese, England, Sept., 1953 ; on Australian cheese (incl. hypopus), England, Sept., 1953 ; on Cheshire cheese (incl. hypopus), Liverpool, Lancs., Sept., 1953 ; from bird's nest (unident.), Slough, Bucks., 1954 ; farm granary, Bucks., 1954 ; hay in farm store (incl. hypopus), Northants., Aug., 1955 ; from pigeon's nest, Chelmsford, Essex, Nov., 1956.

(iv) United States National Museum Collection Washington (in part) :

On onions from Morocco, imported into Boston, U.S.A., March, 1935 ; on rose flowers from Bermuda, imported into Boston, U.S.A., Aug., 1936 ; in potato cellar, Idaho, U.S.A., May, 1951 ; on tulip bulbs from England, imported into New York, 1949 ; on dahlia tubers from France imported into San Juan (?) U.S.A., 1956.

Misidentifications attributable to *A. farris* (Ouds.)

Adult form :

Berlese, A. (1884). As *Tyroglyphus farinae* (Degeer) Gervais.
Knülle, W. (1963). As Mehlmilbe formen A.

Hypopal form :

Michael, A. D. (1903). As *Tyroglyphus longior* Gervais.
Oudemans, A. C. (1905). As *Aleurobius farinae* L.
Oudemans, A. C. (1905). As *Tyroglyphus dimidiatus* (Herm).
Jary, S. G. (1936). As *Aleurobius farinae* Koch.

Oboussier, H. (1939). As *Tyroglyphus dimidiatus* (Herm.)
Zachvatkin, A. A. (1941). As *Tyroglyphus farinae* (L.)
Hughes, A. M. (1948). As *Tyroglyphus farinae* (L.)
Türk, E., & Türk, F. (1957). As *Tyroglyphus farinae* (L.)
Knülle, W. (1959). As *Acarus siro* L.
Hughes, T. E. (1959). As *Acarus siro* L.
Hughes, A. M. (1961). As *Acarus siro* L.

Material deposited in National Museums

(i) British Museum (Natural History):

Three males, four females and three hypopi, on nine slides labelled : Base of barley stack in field, Abingdon, Wilts., U.K., July, 1959, Collr. D. A. Griffiths, registration number ; 1963.8.19.1-9. One female : In garden humus (compost-heap), Slough, Bucks., U.K., Aug., 1959, Collr. D. A. Griffiths, 1963.8.19.10. About forty hypopi on one slide : Hay in stable, Gloucestershire, U.K., September, 1960, Collr. B. E. Jones, 1963.8.19.11. One male, and twelve specimens, on two slides : Deep litter in chicken house, Hull, E. Yorks., U.K., Oct., 1960, Collr. D. Walton, 1963.8.19.12-13. Two hypopi, on same slide : Home-grown oats, in farm store, Haverfordwest, Pembs., U.K., Nov., 1960, Collr. D. J. Parry, 1963.8.19.14. One male and a female, on same slide : House-sparrow's nest, in out-building, Slough, Bucks., U.K., 20.v.1963, Collr. P. Tyler, 1963.8.19.15. One male, two females and two hypopi, all on one slide, together with some *T. longior* specimens : Spillage in farm granary, Kinangop, Kenya, Elev. 8,100 ft., March, 1962, Collr. C. W. Coombs, 1963.8.19.16.

(ii) United States National Museum, Washington:

Three males, two females and three hypopi, on eight slides : Base of barley stack, in field, Abingdon, Wilts., U.K., July, 1959, Collr. D. A. Griffiths. Twenty hypopi, on one slide : Hay in stable, Gloucestershire, U.K., September, 1960, Collr. B. E. Jones. Four hypopi, on one slide : Deep litter, in chicken house, Hull, E. Yorks., U.K., Oct., 1960, Collr. D. Walton.

Acarus siro Linnaeus, 1758

Acarus siro [var.] *farinae* Linnaeus, C. (1758). *Syst. Nat.* (ed. 10) **1** : 616.
Tyroglyphus farinae Latreille, P. (1796). *Précis Caract. Ins.*: 185.
Aleurobius farinae (L.) var. *africana* Oudemans, A. C. (1906). *Ent. Ber. Amst.* **2** : 43, **syn. n.**

The specific name *farinae*, *Tyroglyphus* Lat., 1796, has been placed on the Official Index of Rejected and Invalid Names in Zoology as being a junior objective synonym of *siro*, *Acarus* L., 1758 through the " First Reviser " selection by Fabricius, J. C. (1794) (Hemming & Noakes, 1958b).

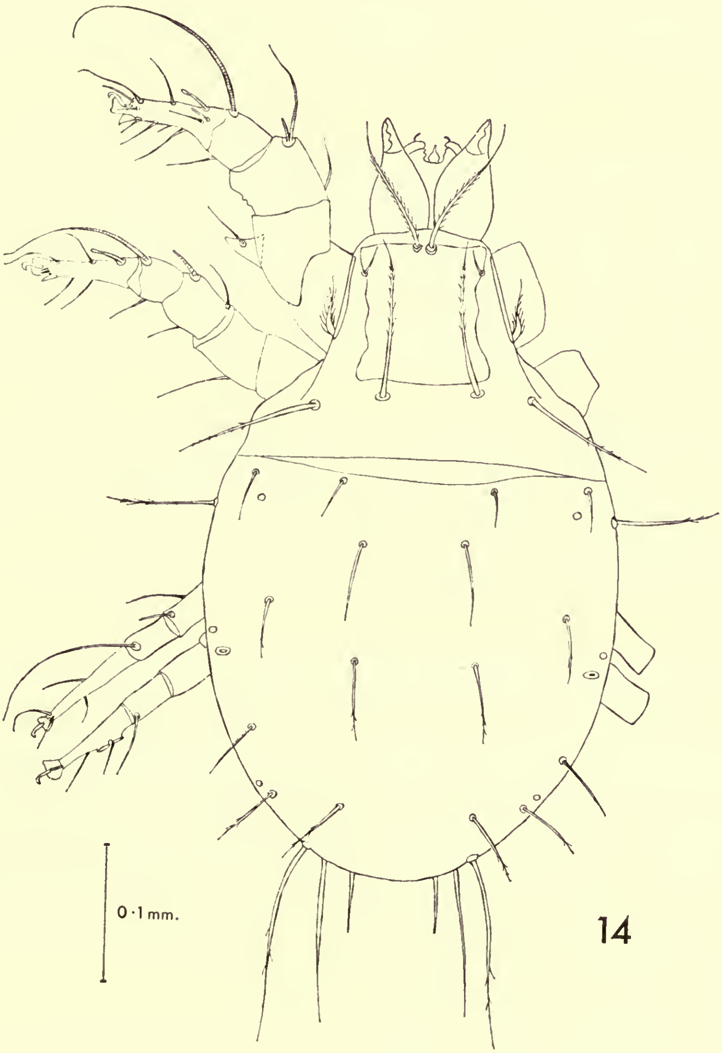
Only one specimen of the variety *africana* was available to Oudemans. This, a female labelled " *Tyroglyphus africana* Ouds., 1906, Type " in Oudemans' own handwriting, is in his collection at Leiden. I have seen the specimen and recognise it to be conspecific with *A. siro* L., 1758.

Type material.

In 1963 I made a search for the type material of *A. siro* [var.] *farinae* L.

I examined Linnaeus' own collection which is housed in the rooms of the Linnaean Society, London. This contains about one dozen large ticks, all without labels and each secured by a pin passing through the body. I am satisfied that not one of these specimens can be considered to be the type material of *A. siro* [var.] *farinae.*

Certain collections which were described by Linnaeus are kept in the museum of Uppsala Academy, Sweden. Dr. Å. Holm, curator of this museum, has informed me that there are no type specimens of Acari in these collections. It is presumed, therefore, that the type material of *A. siro* [var.] *farinae* L., if it ever existed, does so no longer.



14

FIG. 14. *Acarus siro* L. ♂, dorsum.

Neotype designation.

In accordance with the case put forward on page 416, I designate the specimen with the following data as the neotype of *Acarus siro* [var.] *farinae* L., 1758 :
Male ; labelled : Flour residues, Calcot Mill, Berks., U.K., Collr. D. A. Griffiths, 30.v.1963. Right leg II of this male is mounted laterally under a separate coverslip but on the same slide ; mounted in Berlese fluid. Deposited in the British Museum (Natural History) registration number ; 1963.8.19.17.

MALE (Text-fig. 14). Length of idiosoma of six males reared on wheat germ at 90 per cent relative humidity and 20°C = 0.44 mm average. A larger species than *A. farris* with legs and chelicerae possibly more heavily tanned, but again degree of tanning is dependent upon kind of nutrients eaten during growing period and cannot, therefore, be used as a diagnostic character.

This species closely resembles *A. farris* and, in the main, only the differences are given below.

Degree of pectination of idiosomal setae on dorsum similar to *A. farris*, except d_3 and l a also slightly pectinate. Pectinations on scapulars appear to be confined to distal halves of the setae and to be paired. Dorsals d_1 to d_3 stronger and less whip-like. Setal pattern exactly the same as *A. farris* but generally all setae, when expressed as percentage of length of idiosoma, are slightly longer ; sa i is about forty-five per cent of idiosomal length, almost ten per cent longer than sa i of *A. farris*. Also sc e is slightly shorter than sc i, whereas the reverse is true in *A. farris*.

Propodosomal shield present, lateral margin irregular and posterior corners less rounded than in *A. farris*. Grandjeans' organs and supra-coxal setae present.

Setal pattern of venter same as *A. farris* with setae being proportionately slightly longer. Anal and post-anal setae with strong, thick bases as in *A. farris ;* pa_1 and pa_3 with few pectinations, pa_2 smooth.

No discernible differences in morphology of genitalia, apodemes and leg segmentation.

FEMALE (Text-fig. 15). Body larger than male ; setae more sparsely pectinate than male. Propodosomal shield and dorsal idiosomal setal pattern as for male. Anal setae differ from those of *A. farris* ♀ in that a_2 are twice length of a_1, a_4 and a_5 ; also a_3 are almost four times length of a_1, a_4 and a_5 ; pa_2 extend well beyond posterior margin of body with pa_1 about one and a half times longer (Text-fig. 15).

LARVA PROTONYMPH and TRITONYMPH. Dorsal and ventral surfaces of body very similar to *A. farris*. I have not found a character on the idiosoma of these three pre-adult stages which differs sufficiently between *A. siro* and *A. farris* to be diagnostic.

HYPOPUS (Text-figs. 16, 17). This has a motile form.

Body length average of 10 specimens = 0.23 mm.

Colour of live specimens pinkish-beige.

The dorsum is convex with fine irregularly spaced punctations ; divided into propodosoma and hysterosoma ; eyes not present (Text-fig. 16).

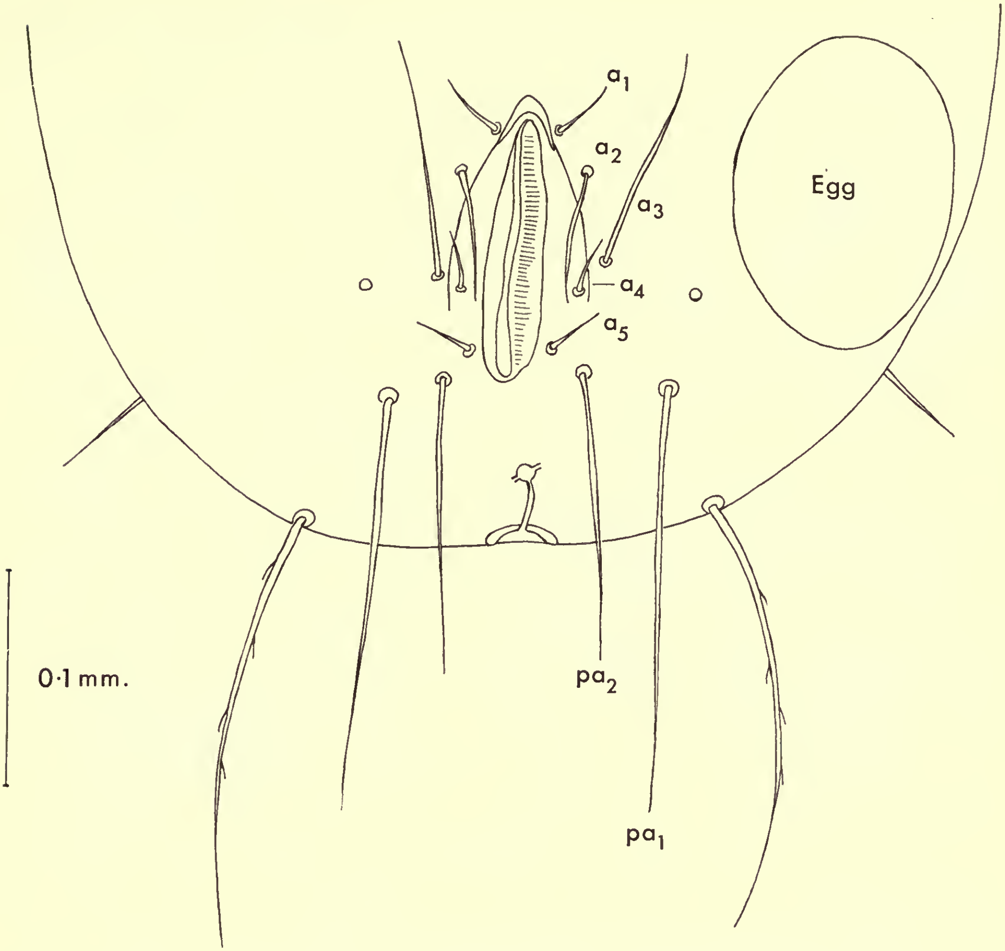


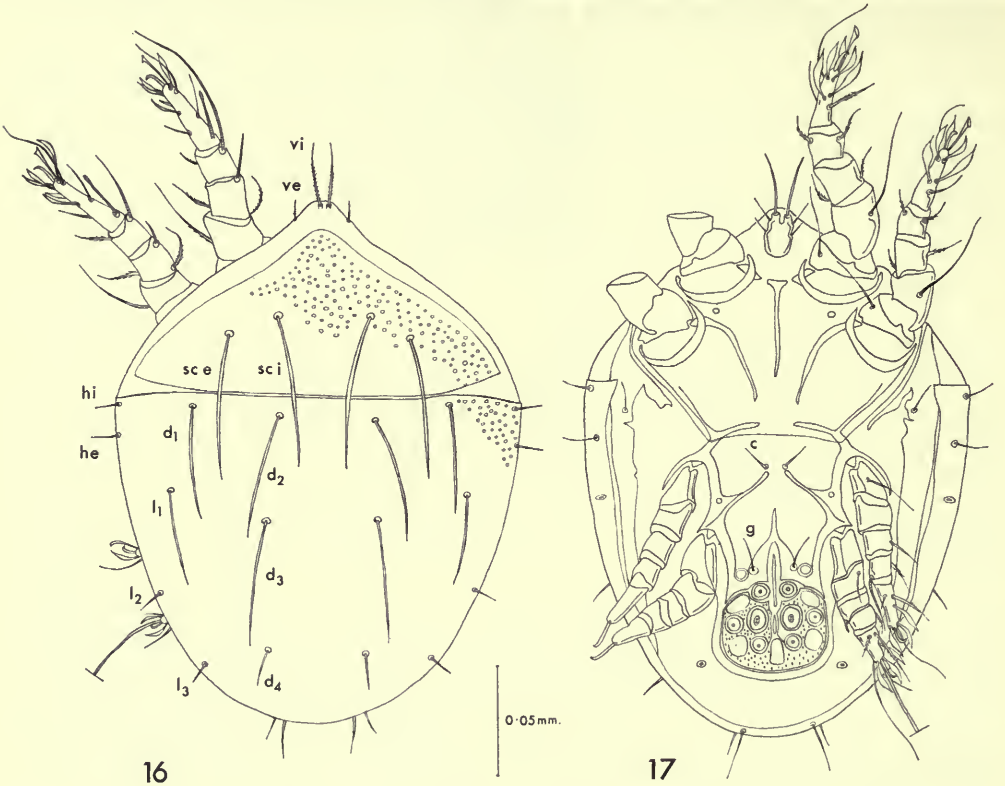
FIG. 15. *Acarus siro* L. ♀, anal region.

Dorsal setal pattern the same as that of *A. farris* but setal shape and lengths are different. Sc e and sc i of propodosoma and d_1, d_2, d_3, and l_1 of hysterosoma are long, flattened and slightly expanded in their middle region. In *A. farris*, these hysterosomal setae are appreciably shorter and barely expanded or flattened. Sc i and sc e are thirty and twenty-eight per cent of idiosomal length respectively. Setae d_2 and d_3 are almost as long as sc i, and just a little longer than d_1 and l_1. Setae d_1 and l_1 are three times longer than d_4 ; in *A. farris* these three setae are about equal in length.

The ventral surface (Text-fig. 17) is very similar to that of *A. farris* except for the following differences which have held true for the many hundreds of specimens I have examined ;

(i) Genital setae arise almost in line with pair of suckers forward of sucker-plate ; bases of seta and sucker on each side of genital opening less than width of setal base apart.

(ii) Apodemes IV barely curved and not sharply angled forward along mid-line.



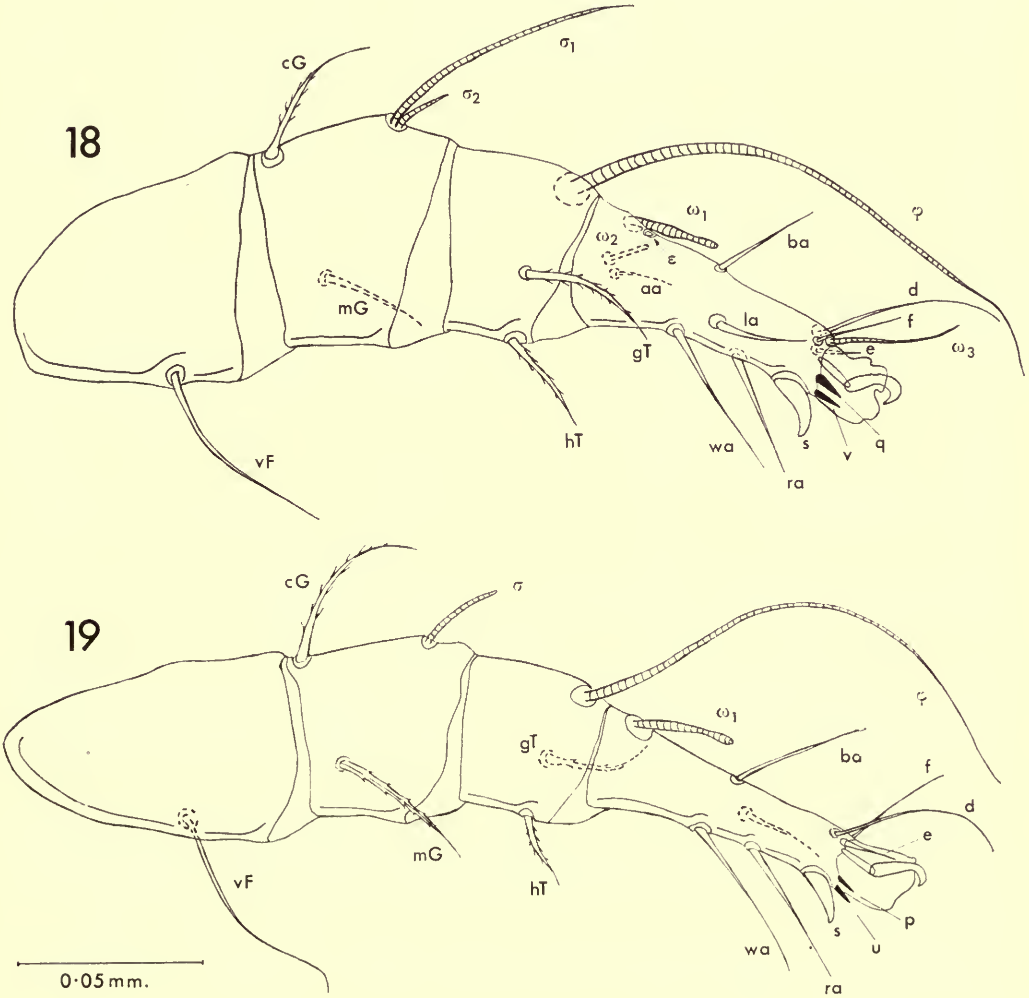
Figs. 16–17. *Acarus siro* L. hypopus. Fig. 16, dorsum. Fig. 17, venter.

Leg chaetotaxy (Text-figs. 18, 19, 21 & 22). The formulae for all the legs of all stages of both setae and solenidia are exactly the same as those given for *A. farris*. Apart from individual variation common to both species, the setal pattern of all stages is also the same except for the position of one seta of the adult, namely ; ba on leg I and II of the adult is situated between and almost equidistant from the base of omega$_1$ and seta d, being slightly nearer omega$_1$ (Text-figs. 18 and 19). In *A. farris*, ba is closer to omega$_1$ (Text-figs. 6 and 7). See also Text-fig. 20, a scatter diagram obtained by plotting ratios of measurements taken from the base of omega$_1$ to ba and from ba to d for populations of *A. siro* and *A. farris*. These ratios appear to hold good regardless of tarsal length, which is very variable.

Pectinations on setae and shape of both setae and solenidia are similar in *A. siro* and *A. farris*, except there is a difference in the shape of omega$_1$ on tarsus I and II of the adult stage. This difference in shape is more pronounced on tarsus II but is not apparent unless a true lateral view of omega$_1$ is obtained.

Omega$_1$ of *A. siro* (Pl. I, fig. 1) is recumbent ; angle between dorsal surface of tarsus and anterior surface of solenidion rarely exceeds forty-five degrees. It is broadest at the base, narrowing to a distinct " goose-neck " before swelling out into a terminal expansion ; width of this expansion at widest part always less than width of widest part of stem. Shape of omega$_1$ of *A. farris* is different in that the stem narrows only imperceptibly before expanding into terminal head and width of head at widest part is about equal to width of widest part of stem (Pl. I, fig. 2).

There is a difference in the shape of omega$_1$ of the hypopus stage. In *A. siro* it is slightly " goose-necked " with a distinct terminal expansion. That of *A. farris* has a terminal expansion barely thicker than widest part of stem.



Figs. 18–19. *Acarus siro* L., ♀ leg chaetotaxy. Fig. 18, leg I—preaxial face. Fig. 19, leg II—postaxial face.

In all other pre-adult stages, except possibly the tritonymph, the shape of omega$_1$ in both species is so similar that it cannot be used to separate the two species.

Considered in proportion to body size, the size of the leg setae (width or length) is not significantly different from those of *A. farris* except in the case of the spine-like seta s. The size of spine s on all legs of all stages (excluding the hypopus and leg I of the male) is greater on *A. siro* specimens than it is on comparable legs of comparable stages of *A. farris* specimens. When the tarsus of *A. siro* is viewed laterally the length of the longest edge (the concave margin) of spine s is equal to the length of the tarsal claw ; the width of the base is almost equal to the length of the shortest edge (the convex margin). In *A. farris* spine s is only about half the length of the tarsal claw and the width of the base is less than half the length of the shortest edge of the spine. Compare Text-figs. 6, 7 with 18 and 19.

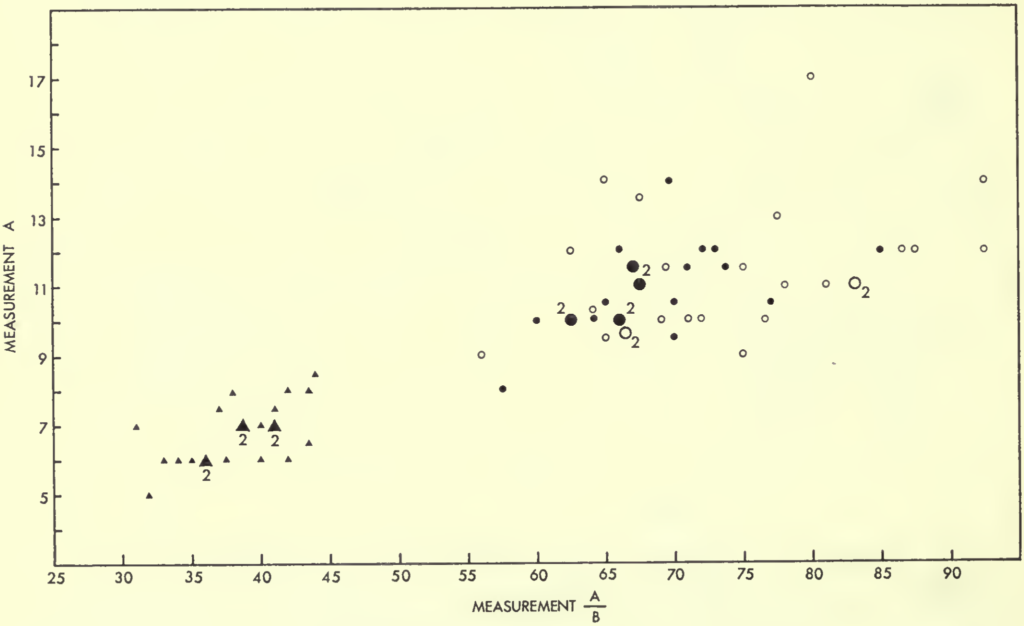


Fig. 20. Scatter diagram showing complete separation of *A. farris* from *A. siro* when measurement A is plotted against A/B. A = distance from base of ω_1 to seta ba ; B = distance from ba to seta d, tarsus II. Closed triangles = *A. farris* individuals. Open and closed circles = *A. siro* from two populations.

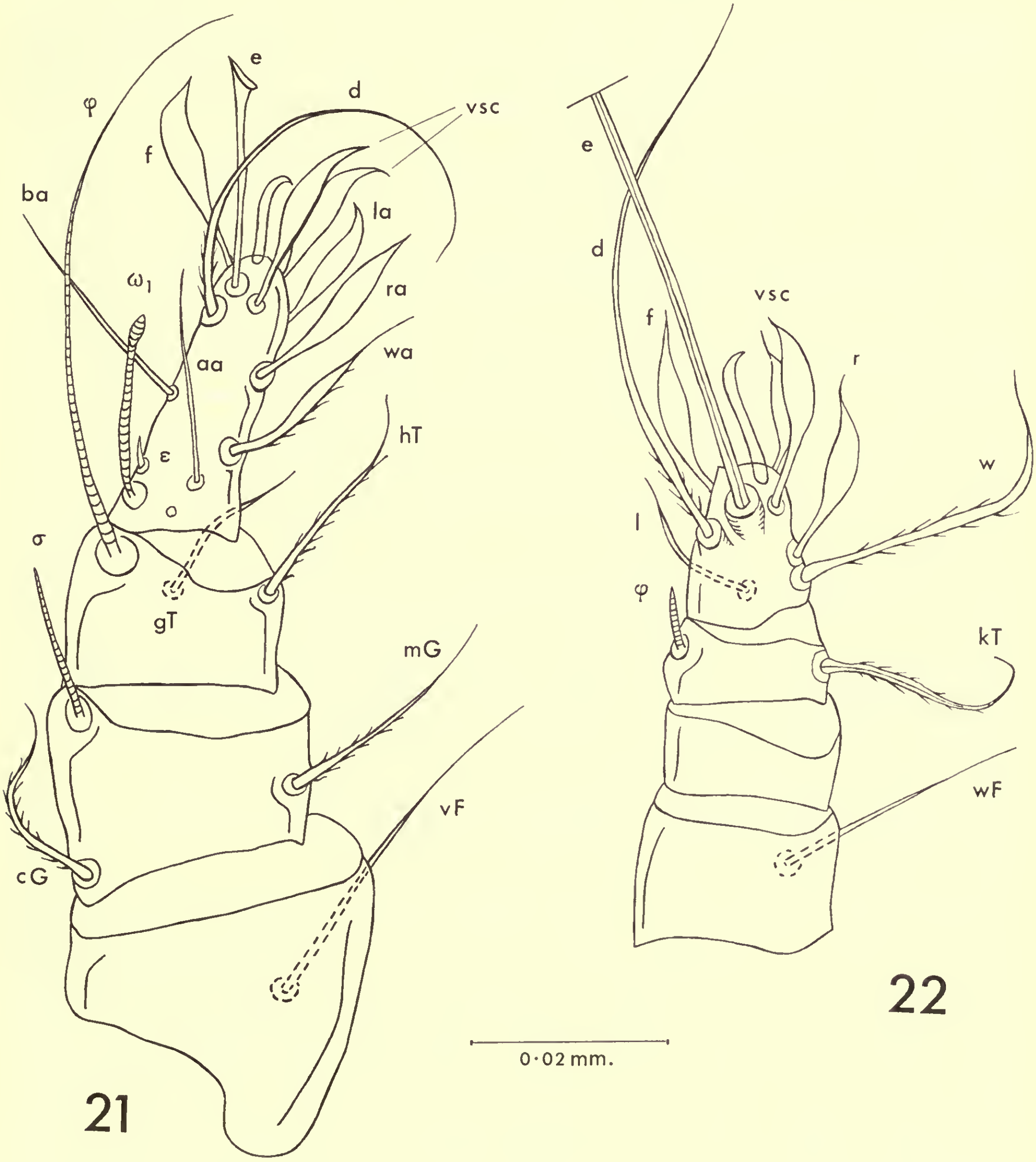
The shape and position of the setae and solenidia (except shape of omega$_1$) on the legs of the *A. siro* hypopus is exactly the same as in *A. farris*. Compare Text-figs. 21, 22 (leg I and IV of *A. siro*) with Text-figs. 10 and 13 (the same legs of the *A. farris* hypopus).

Distribution. England, Scotland, Wales, Northern Ireland, Netherlands, Germany, Kenya, U.S.A., Chile.

Habitat and Locality.

(i) A. C. Oudemans' collection, Leiden :

Arnhem, habitat not given, May, 1898 ; Arnhem, habitat not given, 2.ii.1902 ; corn merchant's wares, Amsterdam, Oct., 1923 ; *Evotomys glareolus*, bank vole (includes one hypopus), Hemmelsdorper See, Holland, 10.iv.1926 ; on pigs intestines, Berlin, 1927 ; on tobacco, Hamburg, Febr., 1928.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0·02 mm.

FIGS. 21–22. *Acarus siro* L., hypopus leg chaetotaxy. Fig. 18, leg I—postaxial face. Fig. 19, leg IV—postaxial face.

(ii) D. A. Griffiths' collection :

A laboratory culture, Pest Infestation Laboratory (P.I.L.), Slough, Bucks., Aug., 1959 ; a laboratory culture, Royal Free Hospital School of Medicine, London, Aug., 1959 ; cultured at P.I.L. (since 1947) Aug., 1959 ; in culture at P.I.L. since 1950, originally from warehouse, Cheshire, Aug., 1959 ; P.I.L. culture, originally from barley meal, Berks., Aug., 1959 ; in culture at P.I.L. since 1957, originally from home-grown (H.G.) wheat on farm, Lancashire, Aug., 1959 ; in domestic supply of rolled oats, Slough, Bucks., Aug., 1959 ; in H.G. barley, on farm, Aberhill, Wilts., Feb., 1960 ; in provender mill spillage, Burnham, Bucks., May, 1960 ; in animal feeding-stuffs (A.F.S.) Slough, Bucks., July, 1960 ; in pig-meal on farm, Helmshore, Lancs., June, 1960 ; in farm A.F.S. store, Boxgrove, Chichester, Sussex, July, 1960 ; in farm A.F.S. store, Fletching, Sussex, July, 1960 ; in flour-mill warehouse, Belfast, N. Ireland, July, 1960 ; in railway A.F.S. store, Axminster, Somersetshire, July, 1960 ; in farm A.F.S. store (including hypopus), Tenterden, Aug., 1960 ; in railway A.F.S. store, Bideford, Devonshire, Aug., 1960 ; in railway A.F.S. store, Newton Poppleford, Devonshire, Aug., 1960 ; in railway A.F.S. store, Monmouthshire, Sept., 1960 ; in baled hay, farm granary, Beverley, E. Yorks., Sept., 1960 ; in A.F.S. store, Pembroke, S. Wales, Sept., 1960 ; in farm store, Chewton Keynsham, Somersetshire, 1960 ; in farm granary, Marlow, Bucks., Oct., 1960 ; in deep litter of poultry house, Hull, E. Yorks., Oct., 1960 ; in domestic flour stocks, Bourne End, Bucks., Nov., 1960 ; in deep litter of poultry house, Dunstable, Beds., Nov., 1960 ; in farm stored H.G. oats, Haverfordwest, Pembs., Nov., 1960 ; in farm stored H.G. barley, Bridgend, Glam., Nov., 1960 ; in H.G. barley, Soulbury, Bucks., Dec., 1960 ; in deep litter of poultry house, Huntingdonshire, May, 1961 ; in H.G. oats from Isle of Man, on Motor Vessel Rema at Plymouth, June, 1961 ; in spillage of railway A.F.S. store, Holsworthy, June, 1961 ; one hypopus in grain in ship ex Vancouver, Canada, at London, Sept., 1962. In grain feed, Tomkins County, New York State, U.S.A., 1953 ; in stored grain, Corvallis, Oregon, U.S.A., March, 1956 ; in stored A.F.S., Oregon, U.S.A., July, 1956.

In farm granary spillage, Kinangop, Kenya (elevation 8,100 ft.), March, 1962 ; in farm granary, North Kinangop, Kenya (elev. 8,150 ft.), March, 1962 ; in farm granary, Mau Summit, Kenya (elev. 8,650 ft.), March, 1962.

(iii) Pest Infestation Lab. (Slough) collection :

In flour, Slough, Bucks., Oct., 1944 ; in flour, Aylesbury, Jan., 1945 ; provender warehouse, Slough, Bucks., Jan., 1945 ; oats in A.F.S. store, Slough, Bucks., Feb., 1945 ; wheat-germ stocks, Slough, Bucks., March, 1945 ; calf food, Slough, Bucks., March, 1945 ; contaminating mite culture (incl. hypopus), Slough, Bucks., March, 1945 ; flour stocks, Slough, Bucks., May, 1945 ; on cheese, Slough, Bucks., July, 1945 ; on macaroni, Slough, Bucks., Aug., 1945 ; H.G. wheat, Sutton Bonington, Leics., Sept., 1945 ; grain store, Slough, Bucks., Jan., 1946 ; grain store, Slough, Bucks., June, 1946 ; hops store, Stone, Staffs., June, 1946 ; grain store (incl hypopus), Slough, Bucks., June, 1947 ; persicaria seeds, Luton, Beds., June, 1947 ; H. G. wheat, Bucks., 1947 ; on dead ♀ chaffinch, Bucks., April, 1948 ; linseed, Derby, Dec., 1948 ; linseed, mustard seed and clover seed, Bishop Stortford, Herts., Dec., 1948 ; maize, Altrincham, Ches., April, 1949 ; maize sievings, Reading, Berks., June, 1949 ; pearl barley, Pudsey, Yorks., June, 1950 ; in house martins' nest, Newport, I.O.W., 1951 ; H.G. grain, Avonmouth, Somerset, March, 1951 ; kitchen cabinet, Heyton, Lancs., May, 1952 ; Cheshire cheese, Liverpool, Sept., 1953 ; farm granary, Bucks., 1954 ; farm granary, Bucks., 1955 ; in custard powder, England, 1956.

(iv) United States National Museum Collection (in part) Washington.

On stored sea-weed, Los Vilos Coq., Chile, June, 1951 ; on cheese, Green Bay, Wisconsin, U.S.A., Jan., 1954 ; in grain dust, Seattle, Washington State, U.S.A., Jan., 1954 ; in dairy cattle feed, Culpepper County, New York State, U.S.A., June, 1957.

PUBLISHED DESCRIPTIONS ATTRIBUTABLE TO *A. siro* L.

Adult form :

Robin, C. (1860). As *Tyroglyphus siro* Lat.
Michael, A. D. (1903). As *Aleurobius farinae* Koch (ex Degeer & Linn.).
Andre, M. (1933). As *Aleurobius farinae* Linn.
Zachvatkin, A. A. (1941). As *Tyroglyphus farinae* L., form *typica*.
Nesbitt, H. H. J. (1945). As *Acarus siro* L.
Robertson, P. L. (1946). As *Tyroglyphus farinae* (Linn.)
Hughes, A. M. (1948). As *Tyroglyphus farinae* (Linn.)
Knülle, W. (1959). As *Acarus siro* L.
Hughes, A. M. (1961). As *Acarus siro* L.
Knülle, W. (1963). As Mehlmilbe, formen B.

Hypopal form :

Schulze, H. (1924). As *Tyroglyphus farinae* (Linn.), Hypopus I.

Material deposited in National Museums

(i) British Museum (Natural History) :

Nine males, twenty-four females and two hypopi, on eight slides labelled with the same data as on neotype slide, British Museum registration numbers ; 1963.9.19. 18-25. About one hundred and thirty specimens (including hypopi) on nine slides labelled : Cultured 10 yrs. Royal Free Hosp. Medical School, London, July, 1959, Collr. A. M. Hughes, 1963.8.19.26-34. Six males, two females, and pre-adults, on five slides labelled : Lab. culture, P.I.L., Slough, Bucks., U.K., Aug., 1959, Collr. D. A. Griffiths, 1963.8.19.35–39. Two males, two females, on one slide labelled : Residues in old provender mill, Burnham, Bucks., U.K., May, 1960, Collr. D. A. Griffiths, 1963.8.19.40. Five nymphs, on one slide labelled : In spillage, warehouse section, flour mill, Belfast, N. Ireland, U.K., 5.vii.1960, Collr. A. Marshall, 1963.8. 19.41. Three females, on one slide labelled : Compound animal feedingstuffs in warehouse, Slough, Bucks., U.K., July, 1960, Collr. D. A. Griffiths, 1963.8.19.42. Twenty adults, on one slide labelled : Residues in a farm store nr. Chichester, Sussex, U.K., July, 1960, Collr. T. McDonald, 1963.8.19.43. Ten adults, on one slide : Residues in a farm feed-store, Fletching, Sussex, U.K., July, 1960, Collr. T. McDonald, 1963.8.19.44. Ten adults and three hypopi, on two slides : Compound animal feedingstuffs in warehouse, Axminster, U.K., 11.viii.1960, Collr. A. S. C. Smith, 1963.8.19.45-46. Twenty adults, on one slide : Compound animal feedingstuffs in warehouse, Bideford, Devon, U.K., Collr. A. S. C. Smith, 1963.8.19.47. One hypopus: Animal feedingstuffs in farm store, Tenterden, U.K., Aug., 1960, Collr. A. M. Hughes, 1963.8.19.48. Eleven adults, on one slide : Compound animal feedingstuffs in warehouse, Monmouth, Wales, U.K., Collr. D. J. Parry, Sept., 1960, 1963.8.19.49. About ten adults, one slide : Self-raising flour in house, Bourne End, Bucks., U.K., 4.xi.1960, Collr. L. P. Lefkovitch, 1963.8.19.50. Ten adults, on one slide : Compound animal feedingstuffs in warehouse, Pembroke Town, Wales, U.K., Collr. D. J. Parry, 28.ix.1960, 1963.8.19.51. Four adults (*T. longior* also on slide) : Home-grown barley in farm-store, Bridgend, Glam., U.K., Nov., 1960, Collr. D. J. Parry, 1963.8.19.52. Three males, two females, on one slide : Home-grown barley in grain store, Soulbury, Bucks., Dec., 1960, Collr. R. W. Howe, 1963.8.19.53. Four females, four males, on two slides : Animal feedingstuffs residues, warehouse, Holsworthy, U.K., June, 1961, Collr. A. S. C. Smith, 1963.8.19.54-55. About one hundred specimens, on one slide : Chicken battery house, Farnham Royal, Bucks., U.K., October, 1962, Collr. G. E. Woodroffe, 1963.8.19.56. About fifty specimens, on one slide : Bagged oat-chaff, provender mill., London, U.K., Collr. E. M. Bland, 1963.8.19.57. Eight specimens, on one slide : Grain residues in flour mill bin, Dumfriesshire, U.K., Collr. J. M. Baynes, 21.vi.1963, 1963.8.19.58. Twelve specimens, on one slide : Barley meal on barn floor, Boxford, Berks., U.K., 2.vii.1963, Collr. N. Hunter, 1963.8.19.59. Twelve specimens, one one slide : Spillage near grinder, Westbrook farm, Berks., U.K., 3.vii.1963, Collr. N. Hunter, 1963.8.19.60. Six specimens, on one slide : Meal spillage, provender mill, Henley, Berks., U.K., 4.vii.1963, Collr. N. Hunter, 1963.8.19.61. Twenty-two specimens, on one slide : Mouldy wheat residues, Manor farm, Tetsworth, Oxon., U.K., 18.vii.1963, Collr. N. Hunter, 1963.8.19.62. One male, three females and one nymph, on two slides : Residues, farm granary, North Kinangop, Kenya, Elev. 8,150 ft., March, 1962, Collr. C. W. Coombs, 1963.8.19.63-64. One female : Residues, farm granary, Mau summit, Kenya, Elev. 8,650 ft., March 1962, Collr. C. W. Coombs, 1963.8.19.65. Sixteen specimens, on one slide : In stored feed, Corvallis, Oregon, U.S.A., March 21, 1956, Collr. G. W. Krantz, 1963.8.19.66.

(ii) United States National Museum, Washington :

Three males, ten females, on three slides with the same data as the neotype specimen. Two males, two females and two hypopi, on six slides : Cultured 10 yrs. Royal Free Hosp. Medical School, London, July, 1959, Collr. A. M. Hughes. Seven adults, on one slide : Residues in farm store nr. Chichester, Sussex, U.K., July, 1960, Collr. T. McDonald. Eighteen specimens, on one slide : Residues in farm feed-store, Fletching, Sussex, U.K., July, 1960, Collr. T. McDonald. Five hypopi, on one slide : Compound animal feedingstuffs, in warehouse, Axminster, U.K., 11.viii.1960, Collr. A. S. C. Smith. Five adults, on one slide : Compound animal feedingstuffs, in warehouse, Pembroke Town, Wales, 28.ix.1960, Collr. D. J. Parry. Two males, on one slide : Home-grown barley in store, Soulbury, Bucks., U.K., Dec., 1960, Collr. R. W. Howe. Four males, on one slide : Animal feedingstuffs residues, warehouse, Holsworthy, U.K., June, 1961, Collr. A. S. C. Smith. One female : Residues, farm granary, North Kinangop, Kenya, Elev. 8,150 ft., March, 1962, Collr. C. W. Coombs.

Male and female on same slide : Residues, farm granary, Mau summit, Kenya, Elev. 8,650 ft., March 1962, Collr. C. W. Coombs.

Acarus immobilis sp. n.

ADULT, TRITONYMPH, PROTONYMPH and LARVA. (Text-figs. 24, 25). Morphology of all stages except the hypopus closely resembles the corresponding stages of *A. farris*. I have been unable to detect any diagnostic differences in colour, shape, body size, or setation of the body.

A multivariate discriminant analysis, using four associated measurements was employed on two populations of *A. immobilis* and one of *A. farris* in an attempt to separate the adults of the two species. The following measurements were made on a total of sixty-three male specimens :

a = body length
b = length of omega$_1$ on tarsus I
c = length of omega$_1$ on tarsus II
d = length of tarsus IV

The measurements were selected from many others of different parts of the body as being the most likely to give a separation suitable for use as a diagnostic character. Text-fig. 23, a graphic presentation of the results of this analysis,

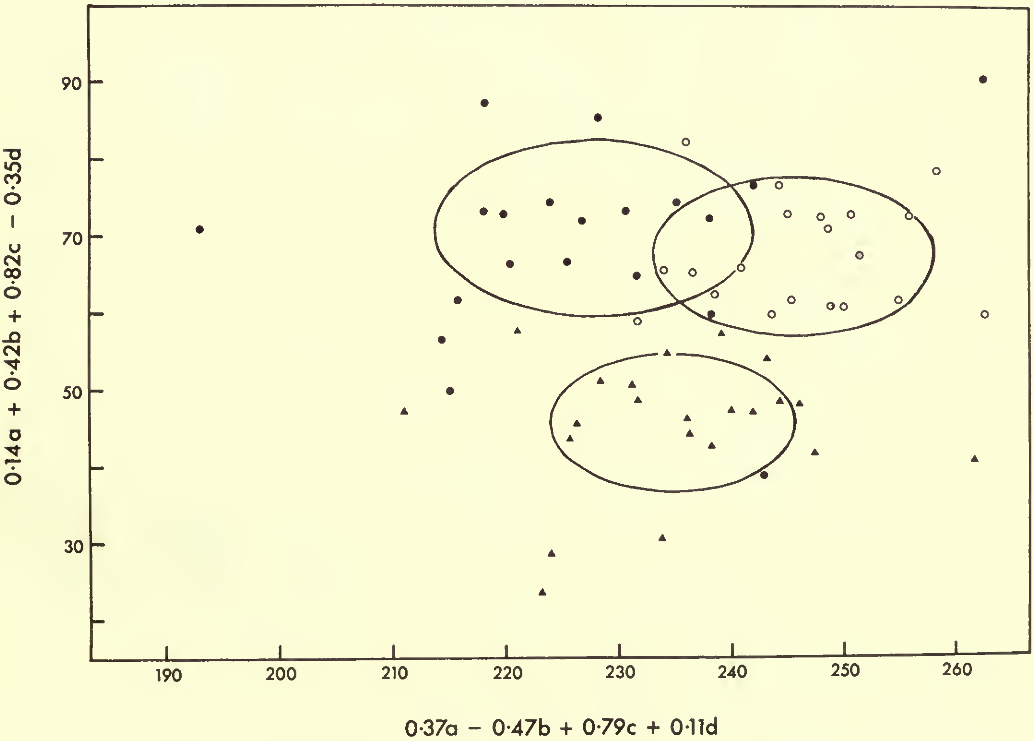
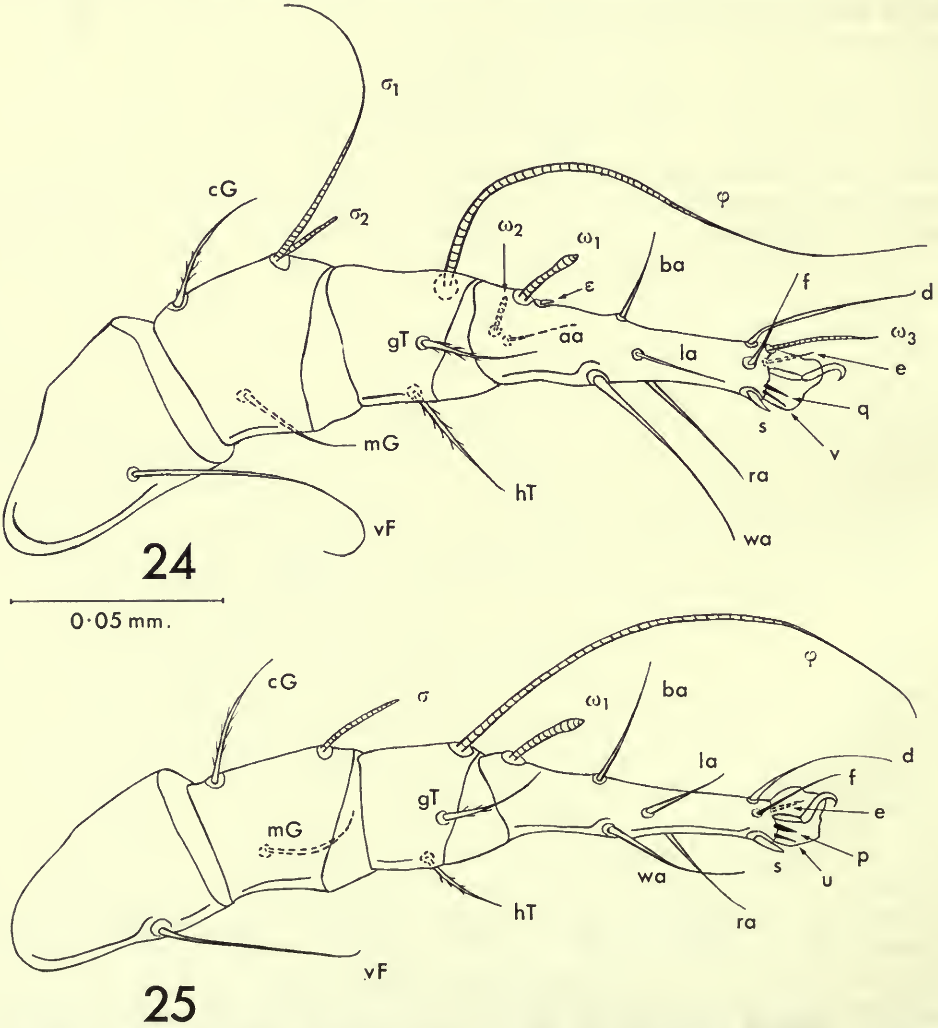


FIG. 23. Diagram illustrating the maximum discrimination possible in two dimensions, based on four measurements upon twenty-one individuals from each of two *A. immobilis* populations and one *A. farris* population.

shows the maximum variation which can be obtained. Although the populations can be seen to be different, over-lap between the species occurs to an extent which precludes the separation of the two species on this basis.

The length of setae on dorsal surface of idiosoma when expressed as a percentage of idiosomal length are indistinguishable from those of *A. farris.* Chaetotaxy of the legs of all stages, except the hypopus, is the same as that for the corresponding stages of *A. farris.* Text-figs. 24 and 25 (legs I and II of the female) demonstrate that the length and shape of setae and solenidia are also very similar to those on specimens of *A. farris,* except for a difference in the shape of omega$_1$ on tarsus I and II of the adults. This difference is more noticeable on the female and, providing a



FIGS. 24–25. *Acarus immobilis* sp. n. ♀ paratype, leg chaetotaxy. Fig. 24, leg I—preaxial face. Fig. 25, leg II—preaxial face.

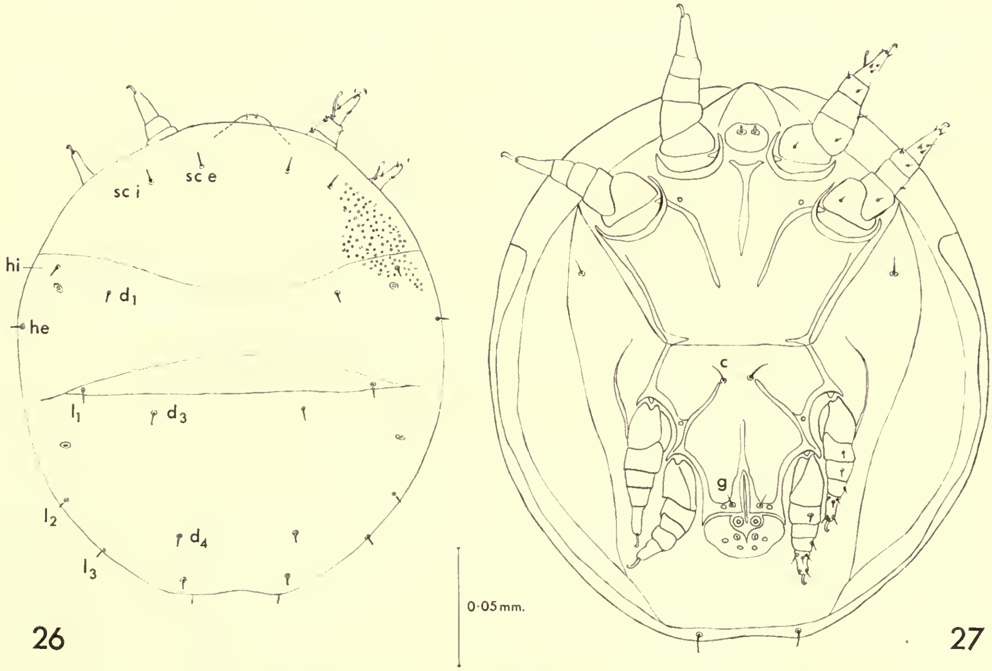
true lateral view is obtained, it is a reliable diagnostic character. In lateral view the sides of the stem of omega$_1$ are virtually parallel, expanding into a distinct egg-shaped terminal head (Plate 1, fig. 4).

The adult forms may be distinguished from *A. siro* employing the same characters which separate *A. siro* and *A. farris*, although spine s of *A. immobilis* appears to be very slightly larger than corresponding spine s of *A. farris*.

Hypopus (Text-figs. 26, 27). The hypopus which is an inert kind has been described by Schulze (1923), Zachvatkin (1941) and Hughes (1955; 1961) under the names *Tyroglyphus farinae* or *Acarus siro*. Phase-contrast microscopy has enabled me to observe certain minute setae on the body and legs which could not have been resolved by the microscopes used by these authors. Consequently, the hypopus stage is re-described below.

Body length : average of 20 specimens = 0.21 mm.

Referred to as the inert hypopal form since the legs are capable of feeble movements only and are unable to support the body, although almost all individuals eventually escape from the protonymphal skin.



Figs. 26–27. *Acarus immobilis* sp. n., hypopus paratypes, Fig. 26, dorsum. Fig. 27, venter.

When viewed from the dorsal surface (Text-fig. 26) the idiosoma is roundly oval, posterior margin rounded or often slightly concave and anterior margin pointed. Surface convex covered with very shallow punctations irregular in size and distribution. Idiosoma divided into a distinct propodosoma and hysterosoma. Eyes not present.

Chaetotaxy of dorsal surface very similar to motile forms except setae v e, d_2 and one pair on posterior margin of hysterosoma are absent. All setae are very short and extremely difficult to see. Hysterosoma bears a pair of circular pores, one behind each of the h i setae and a pair of glands on lateral margin of body on a level with coxae IV.

On ventral surface (Text-fig. 27) the coxal skeleton is well developed, but extremely difficult to follow ; bears close resemblance to coxal skeleton of motile *Acarus* hypopi, being more like *A. siro* in that apodemes IV are almost straight and not bow-shaped as in *A. farris*.

Gnathosoma very much reduced, represented by a hemi-spherical protrusion (situated between coxae I) which bears a pair of very small protuberances each terminating in a short blunt process.

Setae h v present, plus one pair coxal setae above distal ends of epimeres IV and a pair of genital setae either side of anal slit. Two pairs circles in corners of coxal fields I and IV are presumably vestigial coxal suckers.

Sucker plate much reduced, wider than long ; latero-posterior margins indented. Only anterior pair of peripheral suckers are developed, central pair and remaining two pairs of peripherals and pair on either side of genital setae are vestigial.

The leg chaetotaxy of the inert hypopus of *A. immobilis* is much reduced compared with that found on the motile hypopal forms of *A. farris* and *A. siro*. The formula for setae and solenidia of the legs (see Text-figs. 28, 29, 30, 31) is as follows :

Leg I	II	III	IV
(7.2.2.1.1)	(5.2.2.1.1)	(7.1.1.0.1)	(7.1.0.1.0)
	Solenidia (famulus absent)		
(1.1.1.0.0)	(1.1.0.0.0)	(0.1.0.0.0)	(0.1.0.0.0)

On leg I, solenidion omega$_2$, seta e and the ventral spine complex are absent ; omega$_1$ is almost as long as the tarsus, bearing a distinct egg-shaped terminal expansion. Sigma and psi are very short and blunt.

On leg II, setae e, f, aa, ventral spine complex and sigma are absent ; omega$_1$ is again almost length of tarsus.

Chaetotaxy of legs III and IV is the same as for the motile forms except seta e is not present. Psi on these two legs is short and pointed.

Thus, the chaetotaxy of the legs of this inert hypopus is not so very different from that of the motile forms. The major difference is that all the setae of the inert form are spine-like and very much reduced in size. With the exception of omega$_1$, the solenidia are also much smaller. Tarsal claws are well developed.

DISTRIBUTION. England, Scotland, Germany, U.S.A. (possibly France, Italy, Egypt).

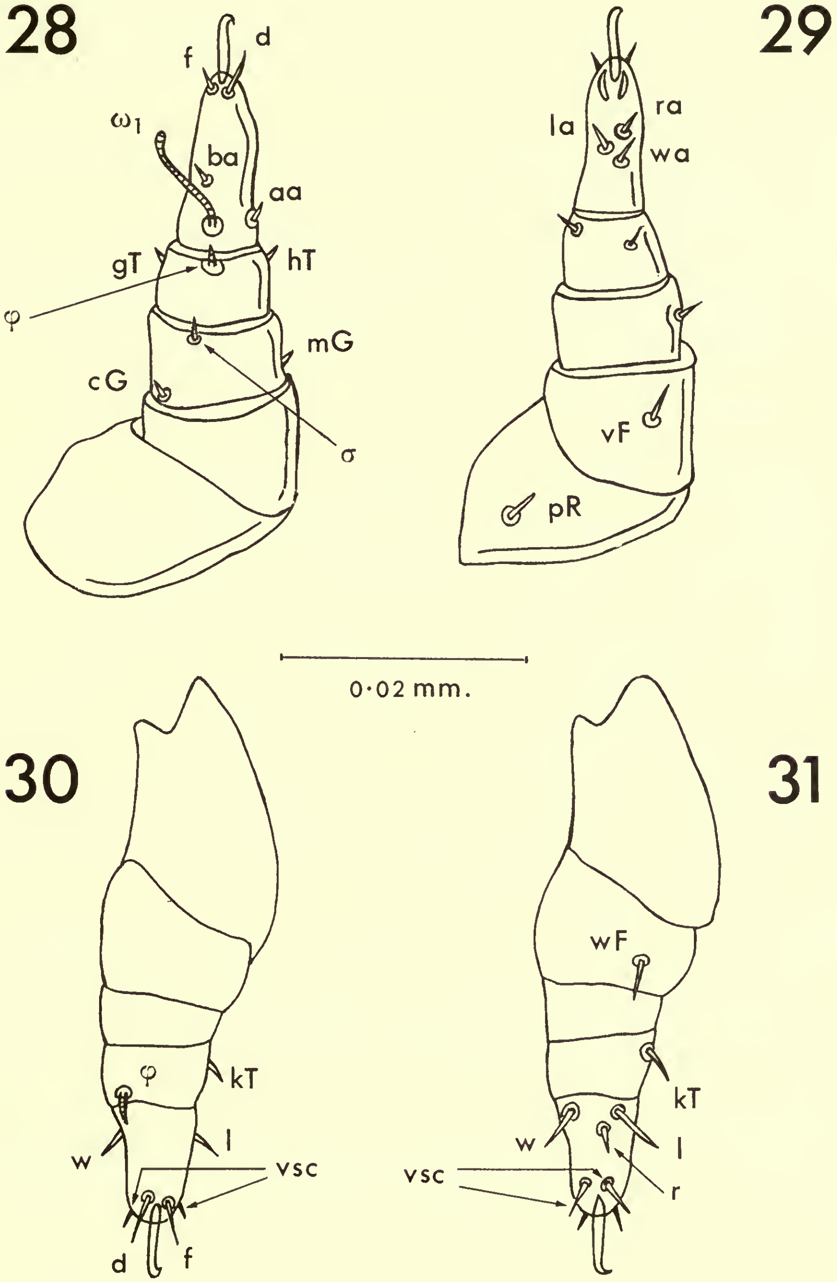
HABITAT AND LOCALITY.

(i) A. C. Oudemans' collection, Leiden :

On a hyacinth bulb, Sassenheim, Feb. 1924.

(ii) D. A. Griffiths' collection :

On imported Northern Manitoba wheat (hypopus), stored at Avonmouth, Sept., 1953 ; in straw at base of crated New Zealand cheese (hypopus), stored at Chatham, Sept., 1953 ; in mouldy grain residues of farm store, (hypopus) Nassington, North-


28
d
f
ω_1
ba
aa
gT
hT
φ
mG
cG
σ
29
ra
la
wa
vF
pR
0·02 mm.
30
φ
kT
w
l
vsc
d
f
31
wF
kT
w
l
vsc
r

FIGS. 28–31. *Acarus immobilis* sp. n., hypopus leg chaetotaxy. Figs. 28–29, right leg I dorsum and venter, respectively. Figs. 30–31, dorsum and venter of right leg IV.

ants., July, 1960 ; in sparrow's nest (including hypopus), nesting box 3, Kinloch farm, Island of Rhum, Scotland, Nov., 1960 ; in hay loft of same farm, July, 1962 ; in H.G. oats, from Isle of Man, on M.V. Rema at Plymouth (including hypopus), June, 1961 ; in grain residues (including hypopus) on M.V. Beavercove, at Victoria Docks, London, May, 1961.

(iii) Pest Infestation Lab. (Slough) collection :

In pigeon's nest, Brentford, Middx., Nov., 1950 ; in grain residues beneath floor of grain silo, Aldershot, Hants., Oct., 1956.

(iv) United States National Museum collection, Washington :

In potato cellar, Arco, Idaho, 17.v.1951 ; on dahlia from Babylon, imported into New York, 31.vi.1934 ; in soil and various plants from Italy, imported into Boston, 1955 ; on potatoes from Egypt, imported into Boston, 1956 ; on *Ginko biloba* from France imported into Washington, 1957.

Misidentifications Attributable to *A. immobilis* sp.n.

Adult form :

Canestrini, G. (1888). As *Aleurobius farinae* Degeer.

Hypopal form :

Schulze, H. (1924). As *Tyroglyphus farinae* (L.) Hypopus II.
Zachvatkin, A. A. (1941). As *Tyroglyphus farinae* (L.)
Hughes, A. M. (1955). As *Acarus siro* L.
Türk, E. & Türk, F. (1957). As *Tyroglyphus farinae* (L.)
Hughes, T. E. (1959). As *Acarus siro* L.
Hughes, A. M. (1961). As *Acarus siro* L.

Material deposited in National Museums

(i) British Museum (Natural History) :

Holotype : Male : Sparrow's nest, box 3, Kinloch Farm, Isle of Rhum, U.K., Collr. P. Wormell, Nov., 1960, 1963.8.19.67, mounted in Berlese fluid.

Paratypes : Five males, twelve females and hypopi, on nineteen slides, with same data as holotype, 1963.8.19.68-86.

Other material : Two males, two females and hypopi, on six slides : Grain residues, Meadow view farm, Nassington, Northants., U.K., July, 1960, Collr. D. A. Griffiths, 1963.8.19.87-92. One female : In straw beneath imported New Zealand cheese, at Chatham, Kent, U.K., Collr. R. W. Howroyd, Sept., 1953, 1963.8.19.93.

(ii) United States National Museum (Washington) :

Paratypes : Three males, six females and hypopi, on eleven slides, with same data as holotype slide.

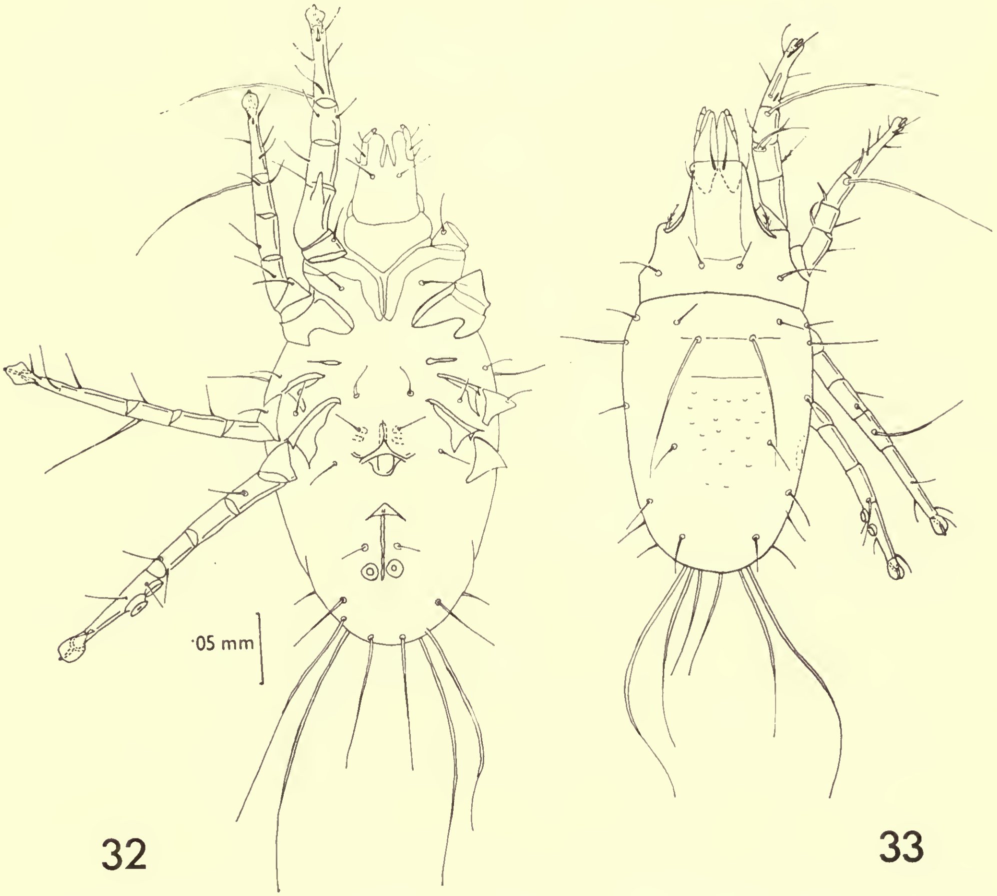
Other material : One male, two females and hypopi, on five slides : Grain residues, Meadow view farm, Nassington, Northants., U.K., July, 1960, Collr. D. A. Griffiths.

Acarus gracilis Hughes, 1957

Type : *Acarus gracilis* Hughes, A. M. (1957). *Ann. Mag. Nat. Hist.* **10** : 753–761, figs.

This species differs from the three species of the *A. siro* complex as follows :

Male (Text-figs. 32, 33). Scapular setae short, about twelve to fifteen per cent of idiosomal length. Setae d_1, d_3, d_4, h i, h v, l a, l p, and sa e shorter than or about equal in length to scapulars ; d_2 more than four times longer than other dorsals. Sa i long, about seventy per cent of idiosomal length. On tarsus IV copulatory suckers are large, fleshy and close together at the base of the segment.



FIGS. 32–33. *Acarus gracilis* Hughes ♂. Fig. 32 venter. Fig. 33, dorsum. Re-drawn from original drawings by A. M. Hughes.

FEMALE (Text-fig. 34 ; Pl. I, fig. 3). Idiosomal setae lengths as for male except that d_3 are longer, more than twice as long as d_1.

In length of setae of anal region it resembles *A. farris* and *A. immobilis* but pa_1 are longer here ; differs from *A. siro* in that a_3 are not more than twice length of a_1 or a_2.

The chaetotaxy of the legs of the adult is very similar to that of the other species except for the shape of $omega_1$. Solenidion $omega_1$ gradually tapers from base to apex, and there is virtually no terminal expansion (Pl. I, fig. 3).

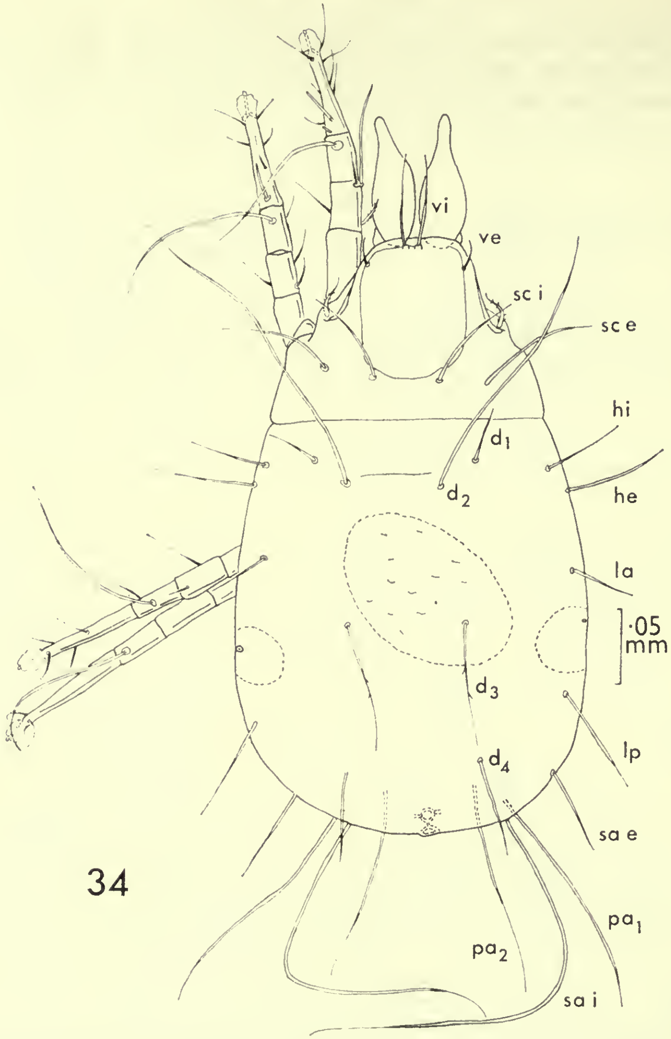


FIG. 34. *Acarus gracilis* Hughes ♀, dorsum. Re-drawn from original drawing by A. M. Hughes.

HYPOPUS (Text-figs. 35, 36, 37, 38 & 39). Is inert in form, closely resembles hypopal form of *A. immobilis* but the following characters are different.

Central pair of suckers are the largest pair on sucker plate ; they are well developed, not vestigial as in *A. immobilis*. Pair of setae on ventral posterior margin of hysterosoma are as long as combined length of tibia IV plus tarsus IV. Coxal skeleton not well developed.

CHAETOTACTIC FORMULAE FOR SETAE AND SOLENIDIA OF THE LEGS :

Leg I	II	III	IV
(7.0.0.0.0)	(6.0.0.0.0)	(8.1.1.0.0)	(8.1.0.0.0)
Solenidia (famulus absent)			
(1.1.1.0.0)	(1.1.0.0.0)	(0.1.0.0.0)	(0.1.0.0.0)

If these formulae are compared with those given for *A. immobilis*, it will be seen that the same solenidia are present in both species but the number of setae on leg segments tibia to trochanter is much less in *A. gracilis*.

The shape and lengths of setae and solenidia (Text-figs. 36–39) are also different from those of *A. immobilis*. Omega$_1$ is short, being not longer than psi of the genu ; many of the tarsal setae are as long or longer than the respective tarsi and often leaf-like in shape. Seta e is present on tarsus III and IV.

DISTRIBUTION. Known from S.E. England only.

HABITAT AND LOCALITY.

(i) Pest Infestation Lab. (Slough) collection:

In bat dung and straw in the attic of a house, near Basingstoke, Hants., October

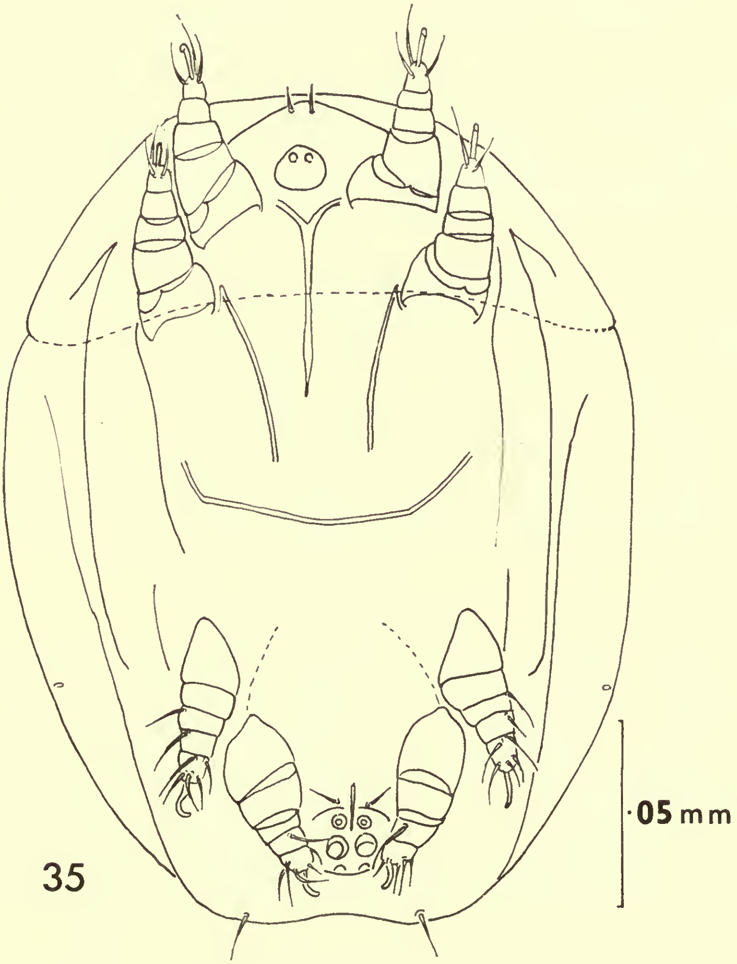
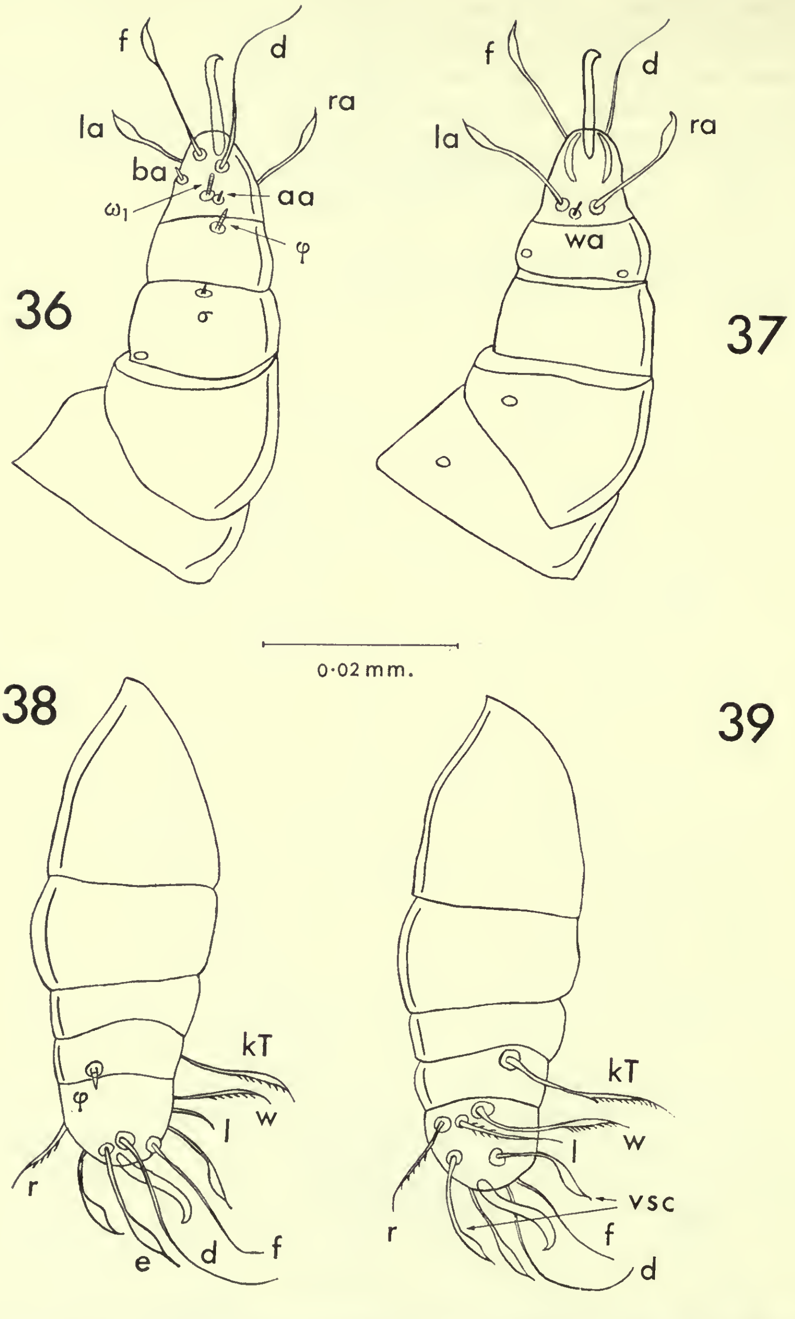


FIG. 35. *Acarus gracilis* Hughes hypopus, ventral view. Re-drawn from original drawing by A. M. Hughes.



36
f
d
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σ
37
f
d
la
ra
wa
0·02 mm.
38
kT
φ
w
l
r
e
d
f
39
kT
w
l
vsc
r
f
d

FIGS. 36–39. *Acarus gracilis* Hughes hypopus, leg chaetotaxy. Figs. 36–37, leg I dorsum and venter, respectively. Figs. 38–39, leg IV dorsum and venter, respectively.

1954 ; in a bat-roost inside a house, Slough, Bucks., July, 1955 ; in old grain debris in attic and first floor of farm granary, Datchet, Bucks., Dec., 1955 ; in residues beneath floor of wheat intake section, flour-mill, Aldershot, Oct., 1956 ; in a bat-roost in a stone tower, Bramshill, Hants., Nov., 1956.

(ii) D. A. Griffiths' collection :

From bird's nest and old nest residues beneath the original tiled roof of a 17th century farmhouse (bats and rats also in residence) near Cumnor, Berks., Sept., 1961.

Acarus tyrophagoides (Zachvatkin, 1941) **comb. n.**

Type : *Tyroglyphus tyrophagoides* Zachvatkin, A. A. (1941). Faune de l'U.R.S.S. Arachnoidea **6** No. 1 : 1–475, figs. *Inst. Zool. Acad. Sc.* Moscow, N.S. No. 28.

The major differences between *A. tyrophagoides* and all other species described above are based on Zachvatkin's original description. Figures 40, 41 and 42 are re-drawn from Zachvatkin (1941).

Scapular setae sc e 1·8 to 3·2 times longer than sc i. Of the hysterosomal setae on the dorsal surface only d_1. d_2, h i and l a are short, from four to thirteen per cent of isiosomal length, whereas all other setae are long, from forty to seventy-five per cent of idiosoma (Text-fig. 40). Thus, in life, adults bear a superficial resemblance to species of the genus *Tyrophagus*. Setae d_3 and d_4 are very long, being about six times longer than d_1 or d_2 (Text-fig. 40).

When viewed laterally, tarsus I of the male bears a swelling on the ventral surface in the region of setae r a and l a (Text-fig. 41).

The supra-coxal setae are long, gently curved and sparsely pectinate (Text-fig. 42).

The hypopus has not been described.

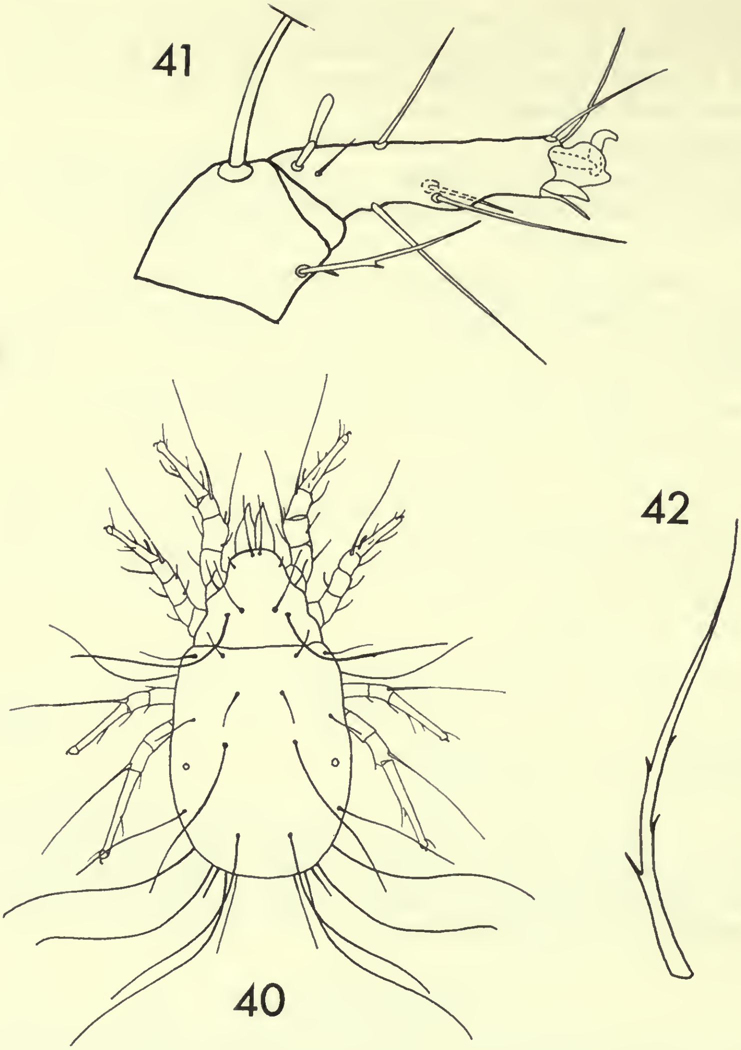
Distribution, Habitat and Locality. This species has been found in Russia only. Zachvatkin (1941) reported that it was taken from the surface layer of soil near a government grain store in the Tartar region. Also from the dead leaf litter of a deciduous forest in the Odessa region. Vysotskaya (1961) found it in the nest of a small mammal (Insectivore) Russia, 1953.

Specimens *incertae sedis*

Virtually all the material of this genus, which has been examined in the past, came from Europe and possibly North America. I have been able to examine small amounts of material which originated, or is believed to have originated, from other parts of the world. The origin of some of the specimens is uncertain because they were collected from produce imported into the U.S.A. or Britain. A small number of these specimens cannot be assigned with certainty to any one of the five species already described. It is considered wiser, at this stage, to list them as specimens *incertae sedis*, although some may be worthy of specific rank. They are catalogued below according to country of origin of the material from which they were taken.

Brazil

Omega$_1$ on tarsus I and II closely resembles that of *A. farris*, but some setae of idiosoma are much longer, especially v i and dorsals. Setae d_2, d_3 and d_4 of this



Figs. 40–42. *Acarus tyrophagoides* (Zach.). Fig. 40, ♀ dorsum. Fig. 41, ♂ tarsus and tibia I—postaxial face. Fig. 43, supra-coxal seta. Re-drawn from Zachvatkin (1941).

specimen all measure more than twenty per cent of the idiosoma. Corresponding setae on *A. farris* specimens are less than ten per cent of idiosomal length.[1]

Material consists of one slide, United States National Museum, Washington. On the left hand label, written in pencil, is :— *Tyroglyphus farinae* Degeer. Right hand label, in black ink is :— On orange navel end, Brazil : At Boston, 8.5.40, Beauchamp ; Boston no. 16017. Lot 40– 18488 (U.S.N.M. number).

[1] Photomicrographs of solenidion sigma$_1$ and histograms illustrating relative lengths of idiosomal setae for all the specimens *incertae sedis* are given in Griffiths (1963) Ph.D. thesis, London University, unpublished.

There are three specimens on the slide ; the centre specimen is *not* an *Acarus*, specimens on left and right are an *Acarus* female and male respectively.

Presumably, these were taken from a cargo discharged at Boston, therefore, cross infestation may have occurred.

New Zealand

Omega$_1$ is very similar in shape but longer than that of *A. immobilis*. Also, all setae of idiosoma except v e are longer, although body length of these specimens are about the same as specimens of *A. immobilis*.

Material, preserved in Oudeman's fluid, was given to me by Dr. A. M. Hughes. It was originally collected from straw beneath New Zealand cheese stored in the London area, July, 1953. The straw presumably originated in this country. The sample also contained inert hypopi identical with those of *A. immobilis*. I have measured the relevant hysterosomal setae of a male and female which Dr. Hughes reared from these hypopi. The setal measurements of this male, when expressed as a percentage of the idiosomal length, closely resembles those obtained from other populations of *A. immobilis*. Measurements made on New Zealand males show that their idiosomal setae are longer, almost ten per cent in some cases. Also, setae sc i are longer than sc e, whereas the opposite is true for *A. immobilis* specimens.

The above evidence suggests that the long setae adults termed " New Zealand " did not give rise to, nor emerge from, the inert hypopi which were found in their company. It may be that *A. immobilis* under different nutritional conditions will be found to have setal lengths which vary to an extent which could include the New Zealand specimens. But, until such information is available, I prefer to consider these long setae adults as specimens *incertae sedis*.

Formosa

The shape of omega$_1$ and relative lengths of the idiosomal setae is extremely similar to the New Zealand specimens. The extra length of the dorsal setae of the Formosan specimens can be accounted for by the fact that the dorsal setae of females tend to be a little longer than those of males.

Data : One slide U.S. National Museum, registration number 56–12672.

Left label : *Tyrophag.* [in pencil]. Right : On *Citrus grandis* fruit, Formosa ; at Phila ; Pa. Oct. 8, 1956, J. Freedland, Collr. Lot 56–12672.

There are two females on the slide ; one still partly enclosed within the tritonymphal skin. Other mites, not *Acarus* or *Tyrophagus*, also on slide.

Japan

Omega$_1$ similar to that of *A. tyrophagoides*. Setae on dorsal surface of idiosoma, except v e and v i, are long, without pectinations and with fine whip-like endings. The train of setae extending behind the opisthosoma bears a superficial resemblance to that of *A. tyrophagoides*. Material differs from *A. tyrophagoides* in that sc i are too long and d_3, d_4 and sa i too short ; no swelling on ventral surface of male tarsus I.

This is possibly a new species, but a description based on two specimens is not considered desirable at this stage.

Data : One slide U.S. National Museum, number 40.21938.

Left label : *Tyroglyphus farinae* Deg. [In pencil]. Right : On *Citrus* sp. Japan : at Seattle, Washington, Oct. 10, 1940, Seattle number 9081 [Black ink].

Azores

Known from one female only. Shape of omega$_1$ and shape and size of spine s is extremely similar to *A. siro*. However, setal histogram is different ; d$_2$ is the longest of the dorsal setae, being three times longer than d$_1$ and about equal in length to the scapular setae. This specimen is discussed in the section below.

Data : One female, U.S. National Museum slide number 56–3596.

Left label : *Tyrophag.* [In pencil]. Right : in, on, around Dasheens, Azores : at New York, Jan. 20, 1956, T. V. Henneberry, Collr. Lot 56–3596 [Black Ink].

Kenya

Known from one female, in my collection. Omega$_1$ and spine s as for Azores female and therefore similar to *A. siro*. However, setal pattern extremely like Azores female and therefore different from *A. siro* specimens.

This specimen was collected by my colleague C. W. Coombs, in grain residues of a farm granary, Kenya, April 1962. *A. siro* specimens were taken from the same material.

The Azores ♀ was taken from dasheens, which are a form of sweet-potato. Thus, both the Azores and Kenya specimens were found in a stored-product habitat. Their close resemblance to *A. siro* suggests that they may possibly be a variation of this species.

China

Omega$_1$ fairly short, expanding gradually into a distinct terminal club, the tip of which is more round than pointed. Seta d$_2$ longest of dorsals ; about twice length of d$_1$. Spine s strong, about two thirds length of tarsal claw but width at base only a quarter of length.

Data : One slide U.S. National Museum, number 37–2183. One male, one female and a female not of *Acarus* on slide.

Left label : *Tyroglyphus farinae* De G. Right : On waterchestnuts, China ; at Chicago, Col. by H. W. Hooker, Jan. 22, 1937.

New Mexico

Known from six slides U.S. National Museum, (only one of which bears a registration number) representing material collected near Santa Fé from two separate but similar habitats, namely, the nests of two small mammals *Perognathus flavus* and *Dipodomys spectabilis*.

The *P. flavus* nest material (36 specimens on one slide) is made up of very small mites with short tarsi. Material from the *D. spectabilis* nest (17 adults on 5 slides) is made up of twelve mites with short cylindrical tarsi as found in the *P. flavus* nest and five adults in which the tarsi are much longer, tapering towards the extremity. Length of the idiosomal setae of these two forms are different in that mites with long tarsi also have longer scapular, dorsal and lateral setae, especially d$_3$, d$_4$ and l$_p$. Since it has been shown (Griffiths, 1963, Ph.D. unpub.) that tarsal length and shape can be influenced by varying the nutritional value of the food given to pre-adult stages, it is considered that these forms probably represent intraspecific variation.

The following characters serve to distinguish these specimens from all others described above. Omega$_1$ long ; from a narrow base it expands gently until, just before the tip, it swells out into a large rounded terminal club. Anal suckers of male minute, their periphery being indistinct. Chelicerae sharply pointed, with sharp, well-defined teeth.

Data : One slide, left label :— *Acarus siro.* Right label : —in *Perognathus flavus* nest, Santa Fé, New Mexico ; Feb. 29, 1952 ; H. B. Morlan Collr., No. 416. Lot 52–1181 (U.S. National Museum Registration Number). Nineteen males and seventeen females.

Five slides ; numbered 806 to 810 inclusive. All labels as follows :— Left label : *Acarus siro.* Right label : Santa Fé, New Mexico, 2 Feb., 1953 ; ex *Dipodomys spectabilis* nest 63A. H. B. Morlan. Total 8 ♂♂ and 9 ♀♀s.

4. ECOLOGY OF *ACARUS*

Published ecological data for the flour mite *A. siro* L., 1758, indicate that this species successfully occupies a wide variety of natural habitats as well as being a serious pest of stored food (Zachvatkin, 1941 ; Sorokin, 1951 ; Woodroffe, 1953 ; Robertson, 1955 ; Griffiths, 1960 ; Boczeck, 1961). An analysis (Appendix II) of the habitat records taken from the text of this paper suggests that this published information is misleading.

For example, from Appendix II, the records for the species making up the *A. siro* complex can be expressed thus :

	No. of times *A. siro* complex recorded	% occurrence of each species		
		A. siro	*A. farris*	*A. immobilis*
Stored product environment	93	76·3%	16·1%	7·5%
Out-door habitat	27	11·1%	59·3%	29·6%

The frequency with which each species occurred in one or other of the two environments is :

Species	Total No. of pops. recorded	% of pops. in stored product habitat	% of pops. in out-door habitat
A. siro	74	95·9%	4·1%
A. farris	31	48·4%	51·6%
A. immobilis	15	46·6%	53·4%

There are, therefore, grounds for suggesting that many of the published records of the occurrence of *A. siro* in natural habitats may be based on misidentifications of *A. farris* and *A. immobilis*.

Within the stored product environment, micro-habitat differences separating *A. siro* from *A. farris* and *A. immobilis* show up very clearly when the stored product habitat is sub-divided as follows :—

	No. of times *A. siro* complex recorded	% occurrence of each species		
		A. siro	*A. farris*	*A. immobilis*
Processed cereal products*	35	100 %	0	0
Cereals as whole grains, also hay in farm-stores	38	57·9%	26·3%	15·8%

* Sometimes combined with non-cereal materials.

Ten of the ninety-three populations recorded from stored produce contained two or more species of the *A. siro* complex : *A. siro* and *A. farris* occurred together eight times, *A. farris* and *A. immobilis* once and all three species once. With one exception (deep litter in a poultry house) the infested material was unprocessed cereals. Populations from out-door habitats were each of one species only. Therefore, whole cereals—a natural link between the warehouse and out-door habitats—appear to be the chief zone of hybridization between the three species of the *A. siro* complex.

It seems probable from the above evidence that *A. farris* and *A. immobilis* are out-door species which are often transported, via the farm to storage premises, in parcels of home-grown cereals. Once they have reached the farm granary or warehouse, there seems to be some barrier which prevents them from becoming established in processed cereal products. A possible explanation may lie in the nutritional differences between processed cereals and the food available in natural habitats ; in this connection the occurrence of *A. farris* on cheese (Appendix II) also requires further investigation.

A. siro appears to be the dominant species within the stored product habitat. Unlike the two field species it seems to be capable of living on processed cereals as well as whole grains. Little can be said about the *A. siro* populations taken from out-door habitats (three records as compared with 16 for *A. farris* and eight for *A. immobilis*). These may have originated in food stores and travelled via the farm to the field. It is equally possible that they represent indigenous populations, since *A. siro* must originally have been confined to natural habitats. Further investigations must be made to determine, as far as possible, the distribution and status (indigenous, or secondary) of these field populations.

The motile hypopal form of *A. siro* has been recorded frequently in ecological papers, mainly from out-door habitats. This paper shows that the hypopus of *A. siro* has been described once only (Schulze, 1924) and that the hypopus of *A. farris* has been attributed incorrectly to *A. siro* in no less than six published descriptions of recent years. Further, the habitat records show that fifty-eight per cent of the *A. farris* populations contained hypopi, whereas the figure for *A. siro* was only 6·75 per cent. It is suggested, therefore, that many of the published records concerning the distribution and frequency of occurrence of the *A. siro* hypopus are based on misidentifications of *A. farris*.

The suggestions put forward in the above paragraphs are based on a limited number of records verified by the author. However, the evidence is sufficient to cast a reasonable doubt upon the correctness of results obtained from past surveys of the " Flour mite " and to justify new ecological studies within and outside food storage premises.

A. gracilis, which produces an inert hypopus, has been recorded from south-east England only. The few records available indicate that it is closely associated with bat-roosts (see page 451).

A. tyrophagoides is known from Russia only. It appears to be an out-door species but the authentic records (see page 453) are too few to provide a basis for any speculation as to its micro-habitats.

5. SUMMARY

A neotype is designated for *Acarus siro* [var.] *farinae* L., 1758.

Five species taxa are recognised, one of which was hitherto erroneously placed in synonymy ; another is described for the first time. Keys to five adult and four hypopal forms are provided.

The " Flour mite " represents a complex of three species, namely ; *A. siro* L., 1758, *A. farris* (Ouds., 1905) and *A. immobilis* sp. n.

The hypopi attributed to " *Acarus siro* " are re-described and associated with their correct adult form.

The ecology of the species is reviewed.

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—— 1767. *Syst. Nat.* ed. 12. **1,** p. 1024.

OUDEMANS, A. C. 1905. *Aleurobius farris* nov. sp., Acarologische Aanteekeningen XX. *Ent. Ber. Amst.* **2,** (26), p. 20.

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APPENDIX I

A list of the names appearing in published works which have been considered in the course of this revision.

Bold type is used to indicate the original description of the valid names of the species recognised in this paper.

Most descriptions have been allocated to a genus. The generic name is given in square brackets at the end of the reference. Descriptions which cannot be assigned to a genus are indicated thus [n.a.].

A description allocated to the genus *Acarus* L., 1758 is also assigned to a species when this is possible.

(i) Adult form :

Acarus siro farinae Linnaeus, 1758, *Syst. Nat.* (ed. 10) **reformata 1** : 615.

Acarus siro farinae L., 1758, sensu Fabricius, 1775, *Systemae Entomologie* : 813 . [n.a.]

Käsemilbe, Schrank, 1776. *Beytrag. Naturg.* : 121, tab 6, figs. 2, 3 . . [*Acarus* sp.]

Mitte (sic) de la farine Degeer, 1778. *Mem. pour servir à l'hist. des insectes,* **7** : 97, pl. 5, fig. 15 . . . . [*Acarus* sp.]

Mitte domestique Degeer, 1778. *Mem. pour servir à l'hist. des insectes*, **7** : 88, pl. 5, figs. 2, 3, 4 . . . . [*Glycyphagus*]

Acarus siro Schrank, 1781, in *Augustae Vindelicorum* : 514, pl. 3, fig. 4 . . [*Carpoglyphus*]

Acarus siro L., 1758, sensu Fabricius 1781, *Species Insectorum Exhibientes*, **2** : 489 [*Acarus* sp.]

Acarus siro L., 1758, sensu Fabricius 1794, *Ent. Syst.* **4** : 430 . . . . [*Acarus* sp.]

Acarus siro Linn. Fab. sensu Latreille, 1796, *Précis des carac. gén. des Insectes* etc. : 185 [n.a.]

Acarus siro Linn. sensu Latreille, 1802, Sonnini's ed. *Suites à Buffon*, **7** : 63 . . [n.a.]

Acarus siro sensu Fabricius, 1805, *Syst. Antliat.* : 357 . . . . . [*Glycyphagus*]

Acarus domesticus sensu Latreille, 1806, *Gen. Crust. Ins.*, **1** : 150 . . . [*Glycyphagus*]

Acarus farinae sensu Latreille, 1806, *Gen. Crust. Ins.*, **1** : 151 . . . . . [n.a.]

Acarus siro Fab., sensu Latreille, 1810, *Consid. Gen. Anim. Crust. Ins.* : 132 & 425 [n.a.]

Acarus siro sensu Fabricius, 1822, *Syst. Antliat.* (ed. 2) : 357 . . . . [*Glycyphagus*]

Acarus farinae Degeer sensu Dugés, 1834, *Ann. Sci. Nat.* **2** : 37 . . . . . [n.a.]

Acare (sic) domestique Degeer sensu Dugés, 1834, *Ann. Sci. Nat.* **2** : 37 . . [*Acarus* sp.]

Acarus farinae sensu Sundeval, 1837, *Physiogr. Sällsk. Tidskr.* **1** : 35, figs. 10, 11, 12 [*Acarus* sp.]

Acarus farinae Degeer, sensu Koch 1841, in Panzer *Deuts. Ins.*, Heft 32, 21 . [*Acarus* sp.]

Acarus siro Linn. sensu Koch, 1841, in Panzer *Deuts. Ins.*, Heft 32, 24 . . [*Glycyphagus*]

Acarus siro sensu Sundeval, 1842, *Isis* **35,** fasc. 6 : 445, pl. 2, figs. 10, 12 . [*Glycyphagus*]

Acarus farinae Degeer sensu Gervais, 1844, *Walk. Hist. nat. Ins. Apts.* **3** : 262 . [n.a.]

Tyroglyphus siro (Tyroglyphe domestique) Linn. Degeer sensu Gervais, 1844, *Walk. Hist. nat. Ins. Apts.* **3** : 261, pl. 35, fig. 4 . . . . [n.a.]

Acarus siro Van Leeuwen, 1846, *Nederl. Lancet*, ser. 2, **1,** fasc. 11 : 661, pl. 11, fig. 6 [*Acarus* sp.]

Tyroglyphus siro Lat. sensu Robin, 1860, *Mem. Soc. Nat. Moscou*, **33** : 233, pl. 5, fig. 5, pl. 8 . . . . [*Acarus siro* L.]

Acarus siro Linn. sensu Canestrini & Fanzago, 1877, *Atti. Ist. Veneto.* **4,** (5) : 69 [*Tyrophagus?*]

Tyroglyphus siro Lat. sensu Mégnin, 1880, *Les Parasites et les maladies parasitaires* : 142, fig. 48 . . . . [*Acarus* sp.]

Tyroglyphus farinae (D.G.) Gerv. sensu Berlese, 1884, *Acari, Myriopoda et Scorpiones* etc., Fasc. 14, No. 9, one pl. . . . . [*A. farris*]

Aleurobius farinae Degeer sensu Canestrini, 1888, *Pros. dell' Acar. Ital.*, **3** : 399, pl. 30, fig. 1 . . . . [*A. immobilis*]

Tyroglyphus siro Linn. sensu Canestrini, 1888, *Pros. dell' Acar. Ital.*, **3** : 402, pl. 31, fig. 2 [*Tyrophagus*]

Acarus siro Linn. sensu Oudemans, 1897, *Tijdschr. Ent.*, **40** : 261 . . . [*Tyrophagus*]

Tyroglyphus siro (L.) em. Latr. sensu Canestrini & Kramer, 1899, in *Das Tierreich*, Leif 7 : 141 . . . . [*Tyrophagus?*]

Acarus siro L. sensu Oudemans, 1901, *Tijdschr. Ned. Dierk.*, **1** : 86 . . [*Tyrophagus*]

Tyroglyphus siro (L.) def. by Gerv. sensu Michael, 1903, *British Tyroglyphidae*, **2** : 117, pl. 36, in Ray. Soc. Publ. London . . . . [*Tyrophagus*]

Aleurobius farinae Koch (ex Degeer & Linn.) sensu Michael, 1903, *British Tyroglyphidae*, **2** : 73, pl. 29 . . . . [*Acarus siro*]

Aleurobius farinae (L.) sensu Oudemans, 1905, *Ent. Ber. Amst.*, **1** : 19 . . [*Acarus siro*]

Aleurobius farris Oudemans, 1905, *Ent. Ber. Amst.*, **1** : 20 . . . . [*Acarus farris*]

Aleurobius farinae var. *africana* Oudemans, 1906, *Ent. Ber. Amst.*, **2** : 43 . [*Acarus siro*]

Tyroglyphus casei Oudemans, 1910, *Ent. Ber. Amst.*, **3** : 74 . . . . . [*Tyrophagus*]

Tyroglyphus farris Ouds. 1905 sensu Oudemans, 1913, *Arch. Naturgesch.*, **79,** (10) : 45 [*Acarus farris*]

Acarus siro L. sensu Oudemans, 1913, *Arch. Naturgesch.*, **79,** (10) : 53 . . [*Sarcoptes*]

Tyroglyphus farinae L. sensu Oudemans, 1913, *Arch. Naturgesch.*, **79**, (10) : 61 [*Acarus siro*]

Aleurobius farinae (Degeer) sensu Newstead & Duval, 1918, *Rep. Grain Pests Comm. Roy. Soc.* No. **2** : 6, text-fig. a . . . . [*Acarus farris*]

Aleurobius farinae (Degeer) sensu Newstead & Morris, 1920, *Rep. Grain Pests Comm. Roy. Soc.* No. 8 : 11, pl. 6, figs. 27, 28 . . . . [*Acarus* sp.]

Tyroglyphus farinae (Linné, 1758) sensu Vitzthum, 1929, *Acari*, in *Die Tierwelt Mitteleuropas*, **3** : 73 . . . . [*Acarus* sp.]

Acarus siro (Linné, 1758) sensu Vitzthum, 1929, *Acari*, in *Die Tierwelt Mitteleuropas*, **3** : 88 . . . . [*Sarcoptes*]

Aleurobius farinae (Linn.) sensu André, 1933, *Ann. Epiphyt.*, **19** : 355, 3 figs. [*Acarus siro*]

Tyroglyphus siro L. sensu Jary & Stapley, *Jl. S.E. Agric. Coll.*, **40** : 119 . . [*Tyrophagus*]

Tyroglyphus farinae L. form *typica* sensu Zachvatkin, 1941, *Faune de l'U.R.S.S.* **6** : 86, figs. 91, 113, *Inst. Zool. Acad. Sci. Moscow* . . . . [*Acarus siro*]

Tyroglyphus farinae L. form *farris* sensu Zachvatkin, 1941, *Faune de l'U.R.S.S.*, **6** : 90, figs. 118–120, *Inst. Zool. Acad. Sci. Moscow* . . . . [*Acarus farris*]

Tyroglyphus tyrophagoides Zachvatkin, 1941, *Faune de l'U.R.S.S.*, Arachnoidea **6** No. 1 : 90, figs. 107–111, *Inst. Zool. Acad. Sci. Moscow* . . . . [*Acarus tyrophagoides*]

Acarus siro (Linn.) sensu Nesbitt, 1945, *Canad. J. Res.* (D), 23 : 139, fig. 6 . [*Acarus siro*]

Tyroglyphus farinae (Linn.) sensu Robertson, 1946, *Trans. Proc. Roy. Soc. N.Z.*, **76** : 185, fig. 11 . . . . [*Acarus siro*]

Tyroglyphus farinae (Linn.) sensu Hughes, 1948, *Mites Assoc. with Food Prods. H.M.S.O.* London : 16, fig. 8 . . . . [*Acarus siro*]

Acarus gracilis Hughes, 1957, *Ann. Mag. Nat. Hist.*, **10** : 753, figs. 1, 2, 6, 7, 9, 10

Tyroglyphus farinae (L., 1758) sensu Türk, E. & Türk, F., 1957, *Beitr. Syst. Okol.*, **1**, (1) : 63, figs. 3, 4 . . . . [*Acarus* sp.]

Acarus siro L., 1758, sensu Knülle, 1959, *Mitt. Zool. Mus. Berl.*, **32** : 347, figs. 1, 23 [*Acarus siro*]

Acarus siro (Linn.) sensu Hughes, T. E., 1959, *Mites or the Acari*, London, pl. 7, fig. 2 [*Acarus* sp.]

Acarus siro (Linn.) sensu Hughes, A. M., 1961, *Tech. Bull. No. 9.*, *H.M.S.O.* London : 287, figs. 8, 9 . . . . [*Acarus siro*]

Acarus siro L., form A, sensu Knülle 1963, *Naturwissenschaften* **5** : 1 . . [*A. farris*]

Acarus siro L., form B, sensu Knülle 1963, *Naturwissenschaften* **5** : 1 . . . [*A. siro*]

(ii) The hypopus form:

Tyroglyphus farinae Degeer, sensu Canestrini, 1888, *Pros. dell' Acar. Ital.*, **3** : 399 . [n.a.]

Tyroglyphus longior Gervais sensu Michael, 1903, *British Tyroglyphidae* **2** : 123, pl. 39, figs. 1–4, Ray. Soc. Publ. . . . . [*Acarus farris*]

Aleurobius farinae L. sensu Oudemans, 1905, *Tyjdser Ned. Dierk.*, **8** : 207, pl. 8, figs. 14, 15 [*Acarus farris*]

Tyroglyphus dimidiatus (Herm.) sensu Oudemans, 1905, *Ent. Ber. Amst.*, **1** : 223 [*Acarus farris*]

Aleurobius farinae (Degeer) sensu Newstead & Duval, 1918, *Rep. Grain Pests Comm., Roy. Soc.* No. 2 : 7 . . . . [*Acarus* sp.]

Tyroglyphus longior Gervais sensu Newstead & Morris, 1920, *Rep. Grain Pests Comm., Roy. Soc.* No. 8, pl. 6, fig. 30 . . . . [*Acarus* sp.]

Tyroglyphus farinae (Linn.) sensu Schulze, 1924, *Zbl. Bakt.*, **60** : 536, figs. 1–11 . . [Hypopus I = *A. siro* ; hypopus II = *A. immobilis*]

Aleurobius farinae Koch sensu Jary, 1936, *Ann. Mag. Nat. Hist.*, **10** : 546, fig. [*Acarus farris*]

Tyrophagus dimidiatus (Herm.) sensu Oboussier, 1939, *Z. angew. Ent.*, **26** : 253, fig. 10 [*Acarus farris*]

Tyroglyphus farinae (L.) sensu Zachvatkin, 1941, *Faune de l'U.R.S.S.*, Arachnoidea **6** No. 1 : 86, figs. 67–69 & 57, 58 [Migratory hypopus = *Acarus farris;* resting hypopus = *Acarus immobilis*]

Tyroglyphus farinae (Linn.) sensu Hughes, A. M., 1948, *Mites Assoc. with Stored Food Prods.*, *H.M.S.O.*, London : 16, figs. 12, 13 . . . . [*Acarus farris*]

Acarus siro (L.) sensu Hughes, A. M., 1955, *Ent. Mon. Mag.*, **91** : 99, figs. 1, 2, 3 . . [*Acarus immobilis*]

Tyroglyphus farinae (L., 1758) sensu Türk, E. & Türk, F., 1957, *Beitr. Syst. Okol.*, **1** : 63, figs. 5, 6 . . . . [Wandernymphe = *Acarus farris*]
[Dauernymphe = *Acarus immobilis*]

Acarus siro L. 1758 sensu Knülle, 1959, *Mitt. Zool. Mus. Berl.*, **32** : 347, figs. 27–29 . . [*Acarus farris*]

Acarus siro L. sensu Hughes, T. E., 1959, *Mites or the Acari*, London, pl. 10, figs. 1, 2, 3
[motile hypopus = *Acarus farris*]
[inert hypopus = *Acarus immobilis*]

Acarus siro L. sensu Hughes, A. M., 1961, *Tech. Bull. No.* 9, *H.M.S.O.*, London : 27, figs. 20, 23, 28 . . . . . . [Active hypopus = *Acarus farris*]
[Inert hypopus = *Acarus immobilis*]

APPENDIX II

Analysis of the habitat records which appear in the text under the descriptions of British *Acarus* species. Specimens from all populations were verified by the author.

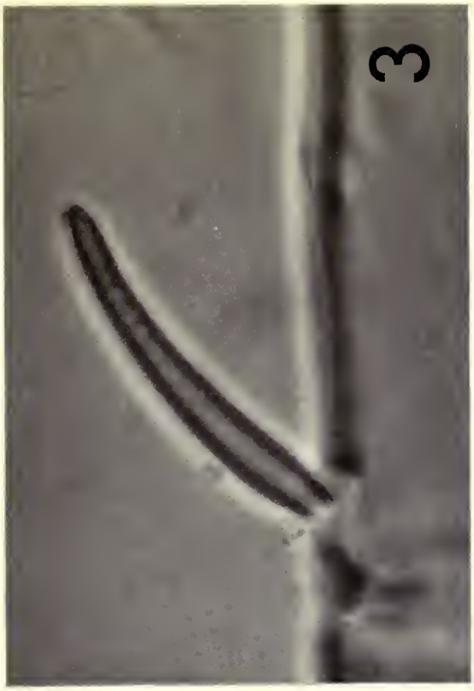
The habitat (location and kind of material)	Number of populations recorded						
	Single species populations				Mixed species populations		
1. THE STORED PRODUCT HABITAT	*A. siro* L.	*A. farris* (Ouds.)	*A. immobilis* sp. n.	*A. gracilis* Hughes	*A. siro* and *A. farris*	*A. farris* and *A. immobilis*	All three species of *A. siro* complex
(a) Materials not stored on farms							
Cereals	12	3	4	1*	3	–	1
Compound animal feeding-stuffs	14	–	–	–	–	–	–
Flour	5	–	–	–	–	–	–
Other household cereal prods.	11	–	–	–	–	–	–
Cheese	2	4	1	–	–	–	–
Non-food prods.	3	–	–	–	–	–	–
Seeds	3	–	–	–	–	–	–
Laboratory cultures (contaminants)	3	–	–	–	–	–	–
(b) Materials stored on farms							
Home grown cereals	8	5	1	–	4	1	–
Compound animal feeding-stuffs	5	–	–	–	–	–	–
Hay	2	2	1	–	–	–	–
Deep litter poultry houses	3	1	–	–	1	–	–
TOTAL	71	15	7	1	8	1	1
2. OUT-DOOR HABITATS							
(a) Associated with animals							
Mammal's nests	–	2	–	–	–	–	–
Bird's nests	1	3	2	–	–	–	–
On mammals or birds	2	1	–	–	–	–	–
Bat roosts and/or attics	–	–	–	5	–	–	–
(b) Other habitats							
In soil ; on plants ; bulbs ; fruit	–	8	6	–	–	–	–
As hypopi on insects	–	2	–	–	–	–	–
TOTAL	3	16	8	5	–	–	
GRAND TOTAL	74	31	15	6	8	1	1

* Taken from grain residues beneath floor of grain intake section of a flour-mill.

PLATE 1

Lateral view of solenidion omega$_1$ (ω_1) situated on tarsus II of the females. Mag. × 2250.

FIG. 1. *Acarus siro* L.
FIG. 2. *Acarus farris* (Oudemans).
FIG. 3. *Acarus gracilis* Hughes.
FIG. 4. *Acarus immobilis* sp. n.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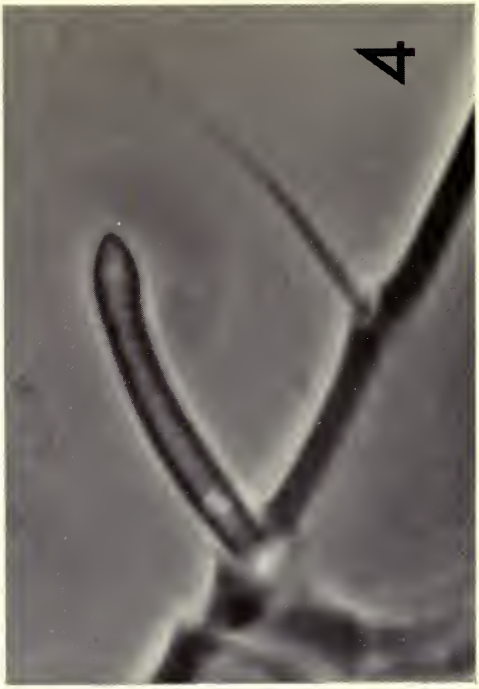
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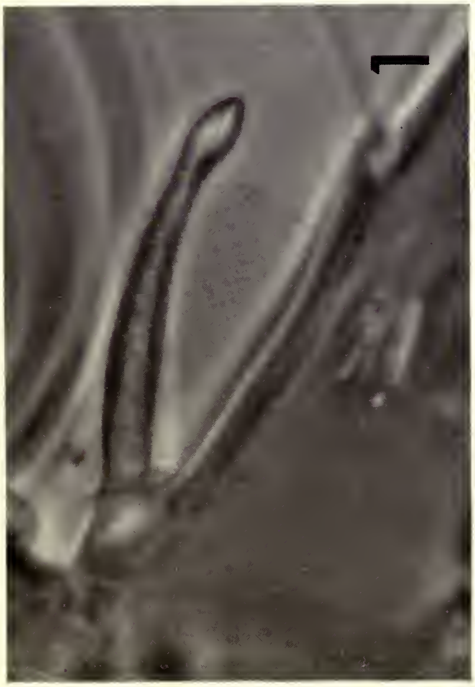
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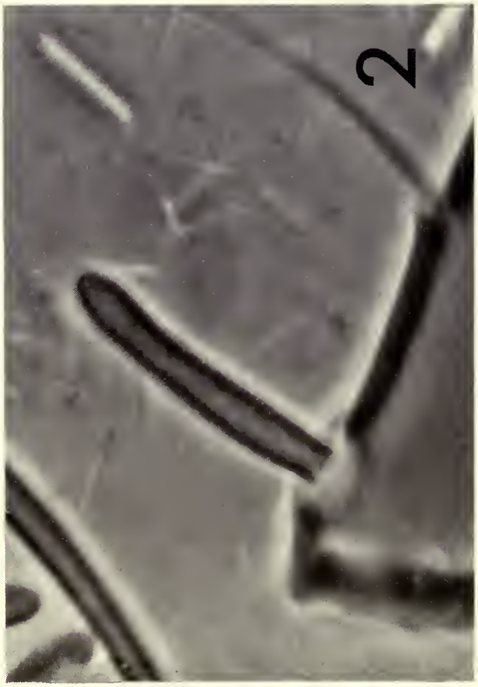
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A COLLECTION OF MESOSTIGMATA (ACARI) ASSOCIATED WITH COLEOPTERA AND HEMIPTERA IN VENEZUELA

K. H. HYATT

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A COLLECTION OF MESOSTIGMATA (ACARI) ASSOCIATED WITH COLEOPTERA AND HEMIPTERA IN VENEZUELA

By K. H. HYATT

The present contribution is based on a collection of mesostigmatid mites associated with Coleoptera and Hemiptera sent to me by Dr. Carlos Díaz-Ungría, Division de Investigaciones Veterinarias, Maracay, Venezuela.

Twenty-six species are described and figured representing the families Uropodellidae, Macrochelidae, Aceosejidae, Laelaptidae, Diarthrophallidae, Hoplomegistidae, Diplogyniidae, Euzerconidae, Klinckowstroemiidae and Paramegistidae. Sixteen species are considered to be new to science. Holotypes, allotypes and some paratypes are deposited in the Collections of the British Museum (Natural History), whilst further paratypes have been returned to Dr. Díaz-Ungría.

Family Uropodellidae

Genus ***UROPODELLA*** Berlese

Uropodella laciniata Berlese

Uropodella laciniata Berlese, A. 1888. Bull. Soc. ent. Ital. **20** : 214, figs.
Uropodella laciniata, Camin, J. H. 1955. Bull. Chicago Acad. Sci. **10** : 65–81, figs.

Berlese (1888) described this species from specimens collected in Argentina, Brazil and Paraguay, and Camin (1955) examined additional specimens from five states in the U.S.A.

The present collection contains a single deutonymph on a hemipteron of the family Reduviidae, *Leogorrus litura* Fabr. (2207), Pie del Cerro, August 1956.

Family Macrochelidae

Genus ***MACROCHELES*** Latreille

Macrocheles amygdaligera f. interrupta (Berlese)

Holocaeleno (sic.) amygdaligera var. interrupta Berlese, A. 1918. Redia **13** : 178.

Evans and Hyatt (1963) record *Macrocheles amygdaligera* (Berlese) from *Phanaeus* spp. (Copridae) in several localities in South America. The present collection contains a single female of *f. interrupta* from *Megacephala carolina* L. (Coleoptera, Cicindelidae) (2330), El Agua, Margarita, 27 August 1956.

Macrocheles dimidiatus Berlese

Macrocheles (*Coprholaspis*) *dimidiatus* Berlese, A. 1918. Redia **13** : 163.

Berlese (1918) examined specimens on *Phanaeus* sp. (Coleoptera, Copridae) and *Bombus* sp. (Hymenoptera) from Argentina. Evans and Hyatt (1963) figured *dimidiatus* and added records from Tennessee (U.S.A.), Mexico, Brazil and Paraguay. The present collection contains six females from *Dichotomius* sp. (Coprinae) (1381), Tacagua, 8 December 1955.

Genus ***GLYPTHOLASPIS*** Filipponi and Pegazzano

Glyptholaspis sp. near ***confusa*** (Foà)

Holostaspis confusus Foà, A. 1900. Bull. Soc. ent. Ital. **32** : 137.
Glyptholaspis confusa, Filipponi, A. and Pegazzano, F. 1960. Redia **45** : 154.

Three females from a beetle (coprófagos 2934), Cabure, 14 December 1957, are very similar to the figures and description of *confusa* given by Filipponi and Pegazzano (1960), but differ in dorsal setae D5–D7 being considerably longer.

Glyptholaspis confusa is previously recorded from La Plata in South America, and from Italy, Bulgaria and England in Europe.

FAMILY ACEOSEJIDAE

Genus ***MELICHARES*** Hering

Melichares (Blattisocius) keegani Fox

Blattisocius keegani Fox, I. 1947. Ann. ent. Soc. Amer. **40** : 599.
Melichares (*Blattisocius*) *keegani*, Evans, G. O. 1958. Proc. zool. Soc. Lond. **131** : 209, figs.

This species is found commonly in insect cultures and in stored foodstuffs infested with various insects.

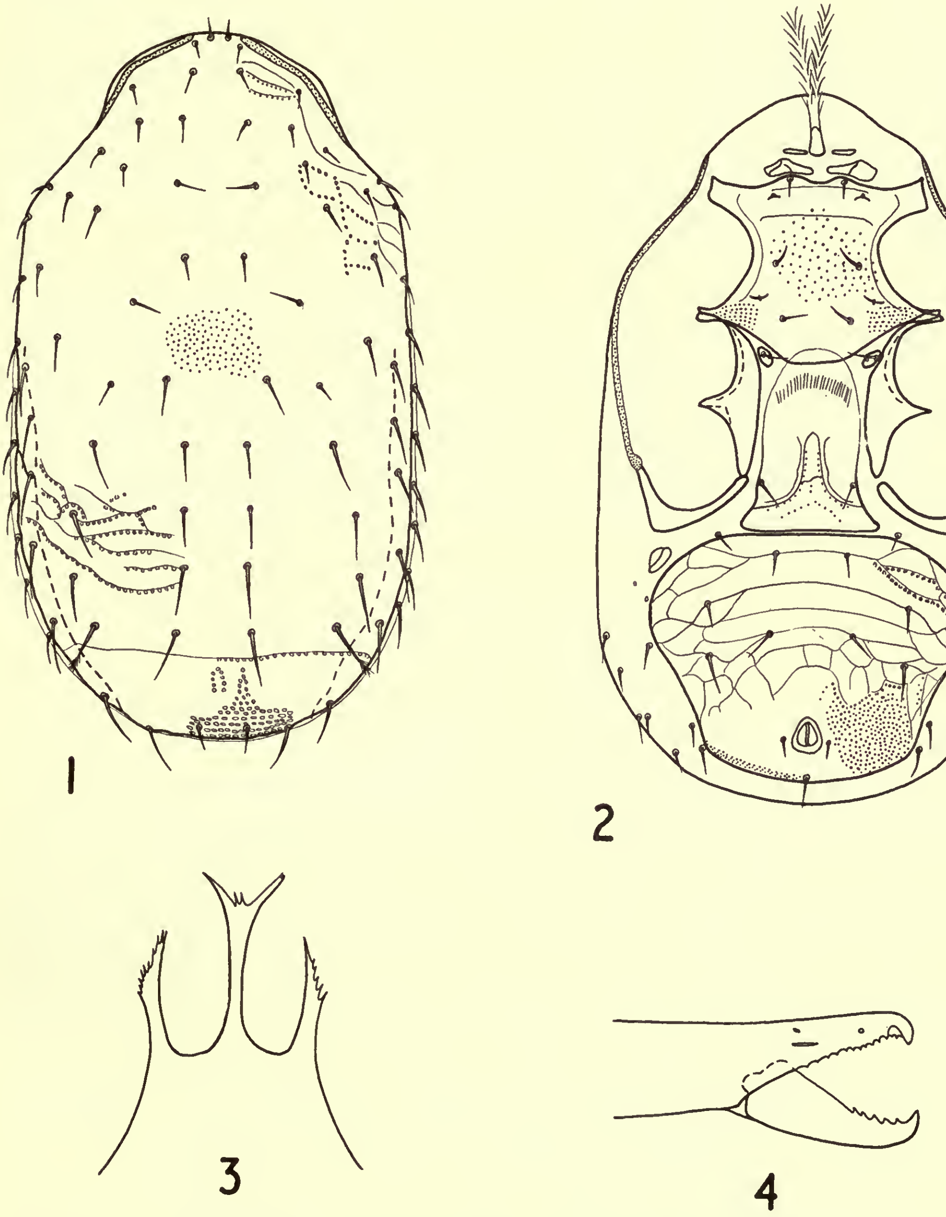
DISTRIBUTION : Fox (1947) recorded this species from Puerto Rico, and Evans (1958) recorded it from Pahang, Malaya. More recently the British Museum (Natural History) has received specimens from Northamptonshire and Sussex, England. The present collection from Venezuela contains specimens from the following beetles : one larva, one protonymph, two deutonymphs, one male and two females from *Golopha porteri* Hope (Coleoptera, Dynastidae) (2185), Camino de Costa Mara, June 1956 ; one male from *Encaladus gigas* Bonelli (Col., Carabinae) (2236), Cerro Atagua, Margarita, 27 August 1956 ; and one male from *Semiotus imperialis* Guèrin (Col., Elateridae) (3669), Mérida, August 1958.

Genus ***ZYGOSEIUS*** Berlese

Zygoseius tectus sp. nov.

FEMALE : Dorsal shield (540–581μ long × 299–330μ wide) ornamented with punctate lines and porose areas (Text-fig. 1). Chaetotaxy comprising 37 pairs of setae of which all are simple and slender, except for one pair towards the posterior margin of the dorsum which is pilose in its distal third.

Tritosternum slender, with a narrow base and pilose laciniae. Sternal shield large, with porose areas ; anterior margin undulating, posterior margin convex, and bearing three pairs of very short setae (Text-fig. 2). Metasternal setae short. Genital shield, with a pair of simple setae, truncated posteriorly, and abutting the



Figs. 1–4. *Zygoseius tectus* sp. nov., female. Fig. 1 dorsal shield. Fig. 2 venter. Fig. 3 tectum. Fig. 4 chelicera.

ventri-anal shield. Endopodal shields opposite coxae III and IV broad and conspicuous. Ventri-anal shield broader than long (196–206μ long × 227–268μ wide) reticulated with porose areas posteriorly, and bearing 11 simple setae. Stigma situated between coxae III and IV, peritreme extending anteriorly almost to the vertical setae ; peritrematal shield extending around coxa IV to meet the endopodal shield. Metapodal plates elliptical. Membrane lateral to ventri-anal shield with eight pairs of simple setae.

Venter of gnathosoma with rostral and internal posterior rostral setae long and slender. Setae of pedipalp simple, apotele two-pronged. Tectum (Text-fig. 3) three-pronged, median prong long and forked, lateral prongs shorter and serrated externally. Dentition of chelicerae (Text-fig. 4) as follows : movable digit with five teeth, fixed digit with about 13 small teeth.

All legs with pulvilli and two claws ; no macrosetae on tarsus IV.

MALE : Unknown.

LOCALITY : The holotype female (1963.10.3.11) and four paratypes (1963.10.3.12–13) associated with *Hololepra humilis* Payk. (Coleoptera, Histeridae) (3207), San Juan de Manapiare, Amazonas, April 1958.

This species differs from the two previously-known members of the genus, *Z. furciger* Berlese, 1916, from South America and South Africa, and *Z. alter* Vitzthum, 1925, from Sumatra, mainly in the ornamentation of the ventral shields, the dentition of the chelicerae, and especially from *furciger* in the form of the tectum.

FAMILY LAELAPTIDAE

Genus ***GAEOLAELAPS*** Trägårdh

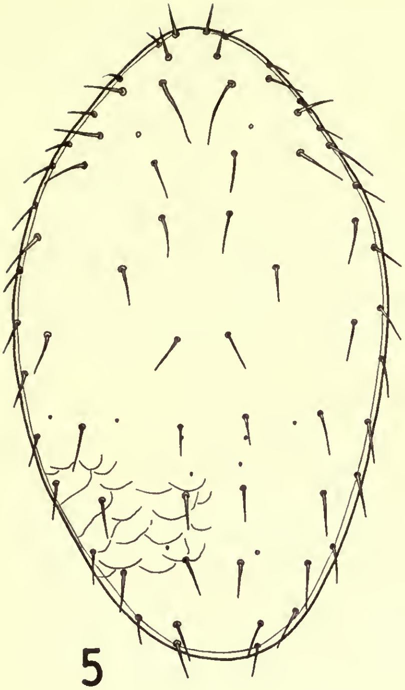
Gaeolaelaps circularis sp. nov.

FEMALE : Dorsal shield (507μ long × 268μ wide) oval in outline, only faintly reticulated, and bearing 33 pairs of simple setae (Text-fig. 5).

Tritosternum small, with pilose laciniae. Pre-endopodal shields weakly sclerotized, but with conspicuous transverse lines. Sternal shield well sclerotized, semicircular posteriorly, and reaching to the anterior third of coxae IV. Reticulations distinct ; the three pairs of sternal setae long (Text-fig. 6). Metasternal setae situated on the membrane posterior to the sternal shield. Genital shield flask shaped, with reticulations, and bearing one pair of simple setae. Anal shield small and bearing the normal three setae associated with the anus. Stigma situated between coxae III and IV, and the peritreme extending beyond coxa I. Membrane posterior to coxae IV with 10 pairs of simple setae. Metapodal plates extremely minute.

Corniculi smooth and slender. Internal posterior rostrals longer than the other three pairs of gnathosomal setae. Chaetotaxy of pedipalp simple. Apotele two-pronged. Tectum (Text-fig. 7) consisting of a single recurved dentate plate. Fixed digit of chelicera with six teeth, movable digit with two teeth (Text-fig. 8).

FIGS. 5–10. *Gaeolaelaps circularis* sp. nov., female. Fig. 5 dorsal shield. Fig. 6 venter. Fig. 7 tectum. Fig. 8 chelicera. Fig. 9 tarsus II. Fig. 10 tarsus IV.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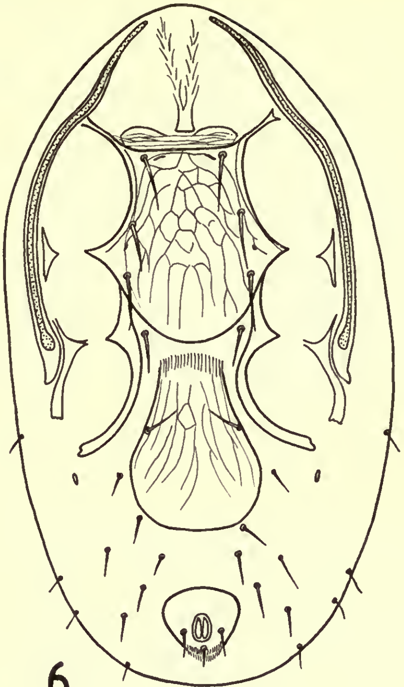
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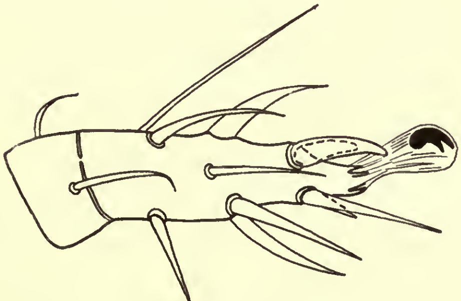
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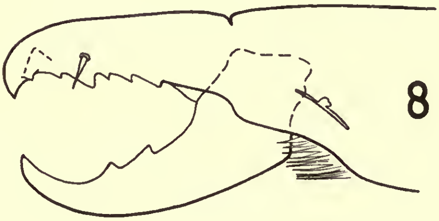
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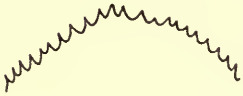
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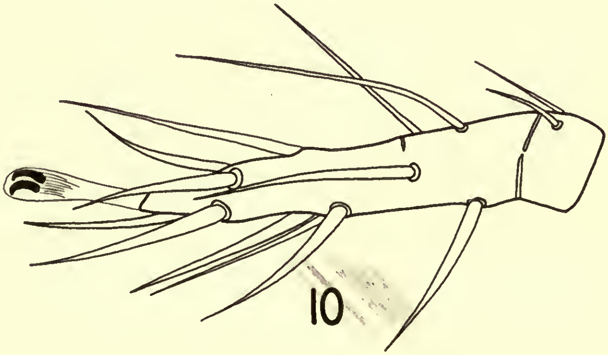
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All setae of leg I fine and simple. Tarsus II with two dorsal spurs distally, and a number of rather stout setae (Text-fig. 9). Tarsus III with a number of stout setae. Tarsus IV slender and with stout setae (Text-fig. 10). All legs provided with pulvilli and two claws.

MALE : Unknown.

LOCALITY : A single female, the holotype (1963.10.3.19), from a passalid beetle (2329), Mérida, 3 December 1957.

This species differs from the two previously known members of the genus, *Gaeolaelaps aculeifer* (Canestrini) 1887, a widely distributed species, and *Gaeolaelaps queenslandicus* (Womersley) 1956 (*comb. nov. : sub. Androlaelaps*), from Queensland, in not possessing a stout spine on femur II, in the shape of the posterior margin of the genital shield, and in the dentition of the chelicerae.

Genus ***HYPOASPIS*** G. Canestrini

Hypoaspis passali sp. nov.

FEMALE : Dorsal shield (764μ long × 477μ wide) with some faint reticulation and bearing about 48–50 pairs of well developed simple setae ; there being some neotrichy posteriorly (Text-fig. 11).

Tritosternum with a narrow base and long pilose laciniae. Pre-endopodal shields very weakly sclerotized and with faint transverse lines. Sternal shield completely covered with faint reticulations and bearing three pairs of long simple setae (Text-fig. 12). Genital shield broadly flask shaped, reticulated and with one pair of simple setae. Anal shield pear shaped and with three simple setae. Stigma situated between coxae III and IV, peritreme extending to the anterior margin of coxa I ; peritrematal shield extending a short distance behind the stigma. Interscutal membrane with up to thirty pairs of setae extending a little anterior to the stigma. Metapodal plates narrow.

Corniculi short and broad. Internal posterior rostrals the longest of the gnathosomal setae. Chaetotaxy of pedipalps consisting of simple setae ; apotele two pronged. Tectum a broad plate with serrated recurved anterior margin (Text-fig. 13). Fixed digit of chelicera with two large and about 12 small teeth movable digit with two teeth (Text-fig. 14).

All legs with a long slender pulvillus and two claws. Chaetotaxy entirely of simple setae, finest on leg I ; stouter setae on legs II to IV.

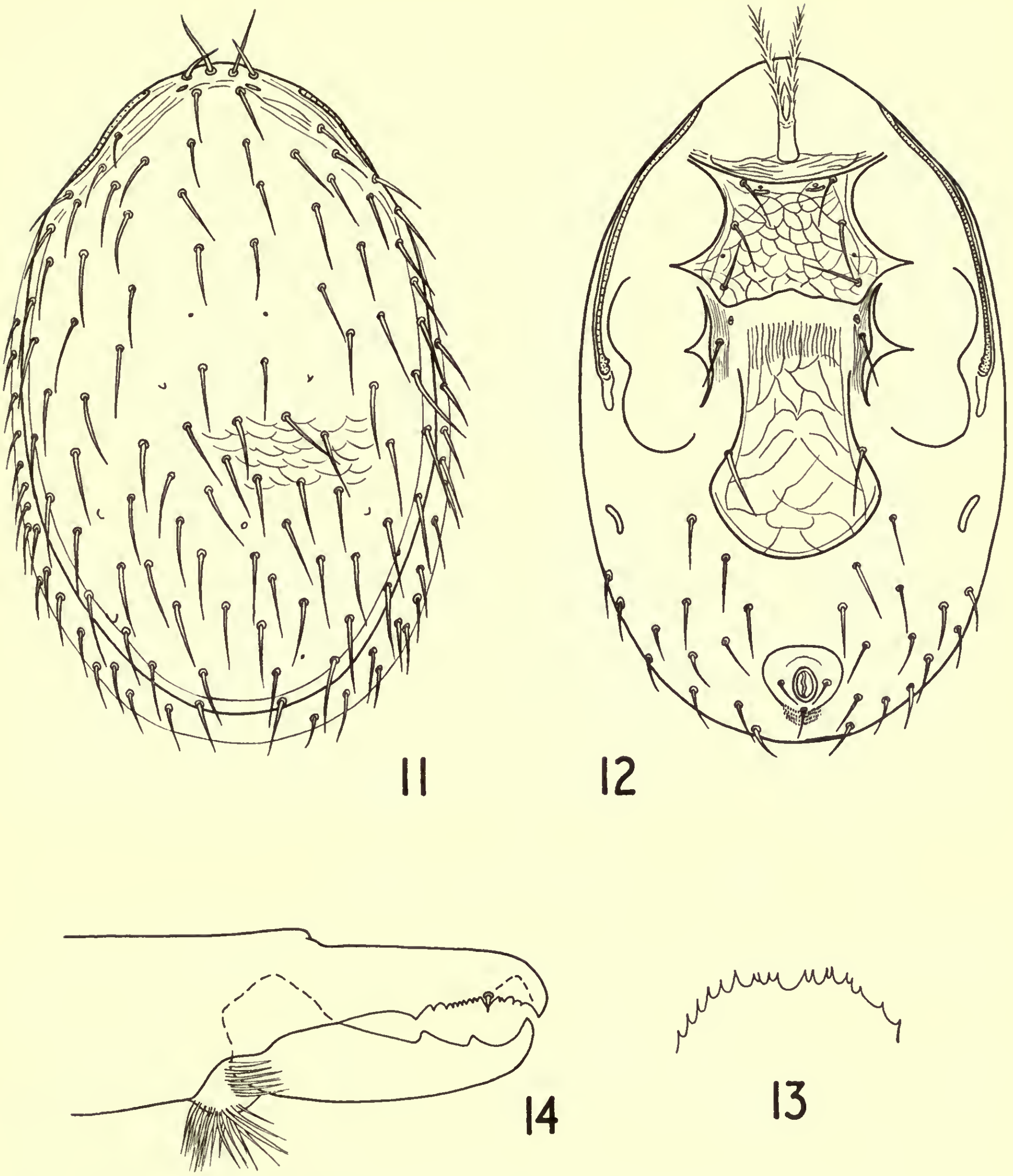
MALE : Unknown.

LOCALITY : A single female, the holotype (1963.10.3.20), from a passalid beetle (2496), Río Caura, Bolívar, Venezuela, May 1957.

Genus ***COLEOLAELAPS*** Berlese

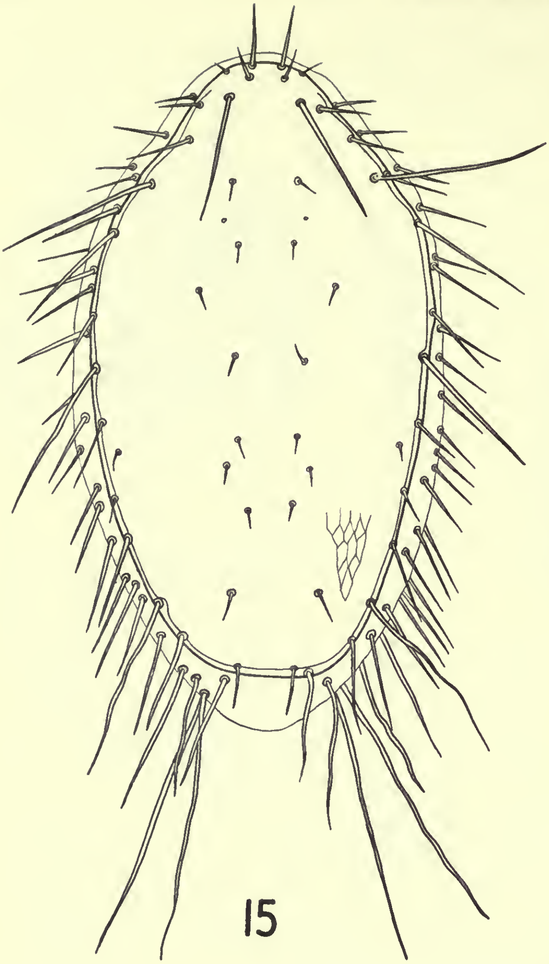
Coleolaelaps metasternalis sp. nov.

FEMALE : Dorsal shield (920–1034μ long × 507–540μ wide) finely granular and with very faint reticulations covering most of its surface, and bearing about 27 pairs of simple setae, the shortest being about 25μ and the longest about 330μ.



Figs. 11–14. *Hypoaspis passali* sp. nov., female. Fig. 11 dorsum. Fig. 12 venter. Fig. 13 tectum. Fig. 14 chelicera.

In the holotype (the figured specimen) one of the posterior dorsal setae is off the shield, though in the majority of the specimens examined it is situated on the edge of the shield (Text-fig. 15).



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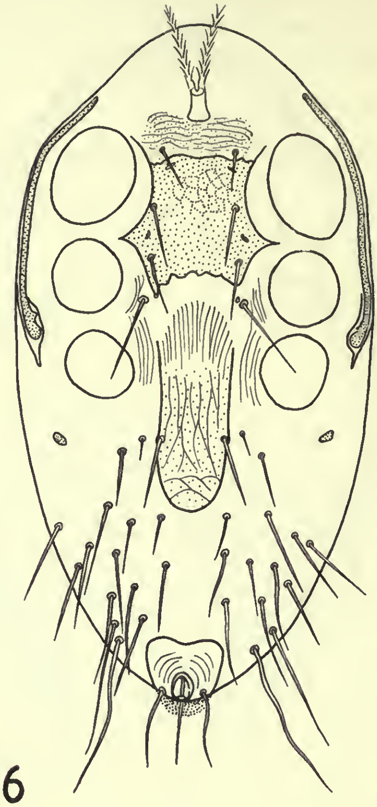

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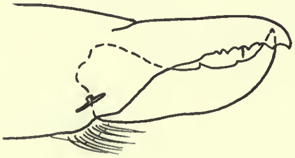

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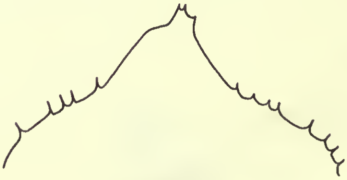

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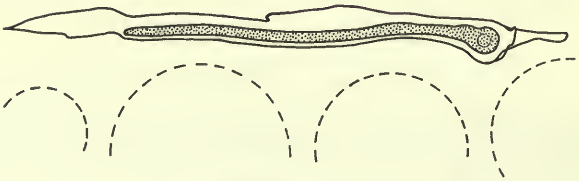

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Tritosternum normal. Pre-endopodal shields very weakly sclerotized, granular and reticulated. Sternal shield finely granular. Sternal setae I apparently off the shield, sternal setae II–III long (Text-fig. 16). Metasternal setae long, situated on the interscutal membrane. Genital shield finely granular and reticulated. Anal shield granular ; the three setae long. Peritreme extending to about the posterior margin of coxa I ; peritrematal shield projecting a little posterior to the stigma (Text-fig. 17). Metapodal shields very small, granular. Membrane posterior to the genital shield with about 15 pairs of setae varying in length ; lateral interscutal membrane with chaetotaxy as in Text-figure 15.

Corniculi short and blunt. Internal posterior rostrals longest of gnathosomal setae. Chaetotaxy of pedipalp simple ; apotele with two prongs. Tectum irregular in outline, partly denticulate (Text-fig. 18). Fixed digit of chelicera with about six small teeth, movable digit with two teeth (Text-fig. 19).

All setae on leg I simple. Tarsus II with five slender spines ; tarsi III and IV each with three slender spines. All legs with a well-developed pulvillus and two claws.

MALE : Unknown.

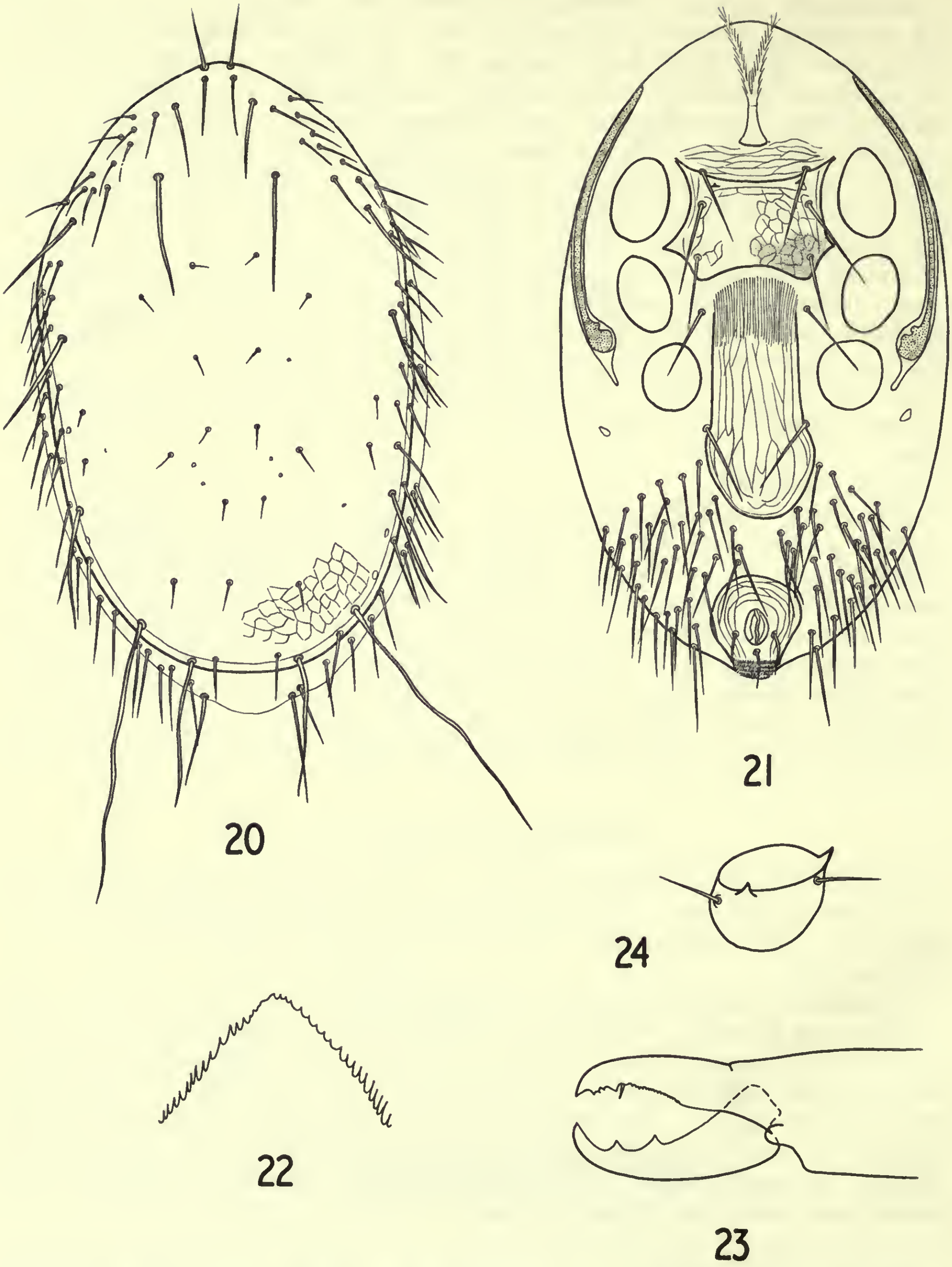
LOCALITIES : The holotype female (1963.10.3.21) and 29 paratypes (1963.10.3.22–31) from a scarabaeid beetle (2184), Cota, 1,000 metres altitude, June 1956 ; one paratype (1963.10.3.32) from a scarabaeid (2167), El Junquito, June 1956 ; 91 paratypes (1963.10.3.33–42) from *Golopha porteri* (Col., Dynastidae) (2183), El Avila, June 1956 ; four paratypes (1963.10.3.43–44) from *Golopha porteri* (2185), Camino de Costa Mara, June 1956 ; 51 paratypes (1963.10.3.45–54) from *Heterogomphus* sp. (Dynastidae) (2186), Chaguaramos, 22 June 1956 ; 11 paratypes (1963.10.3.55–59) from *Golopha porteri* (2851), El Avila, Distrito Federal, June 1957 ; and over 50 paratypes (1963.10.3.60–69) from *Golopha porteri* (2864), Colonia Tovar, August 1957.

Coleolaelaps coxalis sp. nov.

FEMALE : Dorsal shield (880–973μ long × 550–600μ wide) finely granular, with very faint reticulations covering much of its surface, and bearing about 43 pairs of simple setae, the shortest being *c.* 30μ and the longest (one posterior pair) *c.* 450μ (Text-fig. 20).

Tritosternum strongly developed, with long laciniae. Pre-endopodal area weakly granular and striated. Sternal shield with faint reticulations, strongly granular, and with three pairs of long simple setae (Text-fig. 21). Metasternal setae long. Genital shield long and narrow, finely granular and reticulated. Genital setae almost off the shield. Anal shield granular, setae simple. Peritreme extending to about the middle of coxa I ; peritrematal shield projecting a little posterior to the stigma. Metapodal shields very small, granulate. Membrane posterior to the genital shield with over 25 pairs of setae.

FIGS. 15–19. *Coleolaelaps metasternalis* sp. nov., female. Fig. 15 dorsum. Fig. 16 venter. Fig. 17 peritreme. Fig. 18 tectum. Fig. 19 chelicera.



FIGS. 20–24. *Coleolaelaps coxalis* sp. nov., female. Fig. 20 dorsum. Fig. 21 venter. Fig. 22 tectum. Fig. 23 chelicera. Fig. 24 coxa II.

Corniculi long and slender. All gnathosomal setae long, though internal posterior rostrals longest. Chaetotaxy of pedipalp simple ; apotele two pronged. Tectum denticulate (Text-fig. 22). Fixed digit of chelicera with two large teeth and a row of very minute teeth ; movable digit with two large teeth (Text-fig. 23).

All setae on leg I fine and simple. Coxa II with an anteriorly-directed spur (Text-fig. 24) ; tarsus II with three and tibia with two ventral spines ; all setae simple. Tarsus III with three, tibia with two, and genu with two ventral spines ; all setae simple. Tarsus IV with three, tibia with two, genu with one, and femur also with one, ventral spines. Femora II–IV with one long seta. All legs with a pulvillus and two claws.

MALE : Unknown.

LOCALITIES : The holotype female (1963.10.3.70) and over 100 paratypes (1963.10.3.71–80) from *Megosoma elephas* (Col., Dynastidae) (2182), Morón, June 1956 ; and 23 paratypes (1963.10.3.81–90) from *Oryctes* sp. (Col., Scarabaeidae) (1382), El Junquito, 14 December 1955.

Coleolaelaps striatus sp. nov.

FEMALE : Dorsal shield (848–920μ long × 498–550μ wide) finely granular with occasional traces of reticulations, and bearing 30 pairs of simple setae, the shortest being about 38μ and the longest about 240μ (Text-fig. 25).

Tritosternum with well-developed laciniae. Pre-endopodal area weakly sclerotized and granular. Sternal shield characteristically reticulated, pattern arranged longitudinally, finely granulate and bearing three pairs of long setae (Text-fig. 26). Metasternal setae long. Genital shield granular, well reticulated. Anal shield reticulated, setae long. Peritreme extending to about the middle of coxa I ; peritrematal shield tapering a little beyond the stigma. Metapodal shields very small, granulate. Membrane posterior to the genital shield with about 25 pairs of setae.

Corniculi slender. Internal posterior rostrals twice the length of the other gnathosomal setae. Chaetotaxy of pedipalp simple ; apotele with two prongs. Tectum almost completely devoid of denticulations (Text-fig. 27). Fixed digit of chelicera with one large tooth and about eight small ; movable digit with two large teeth (Text-fig. 28).

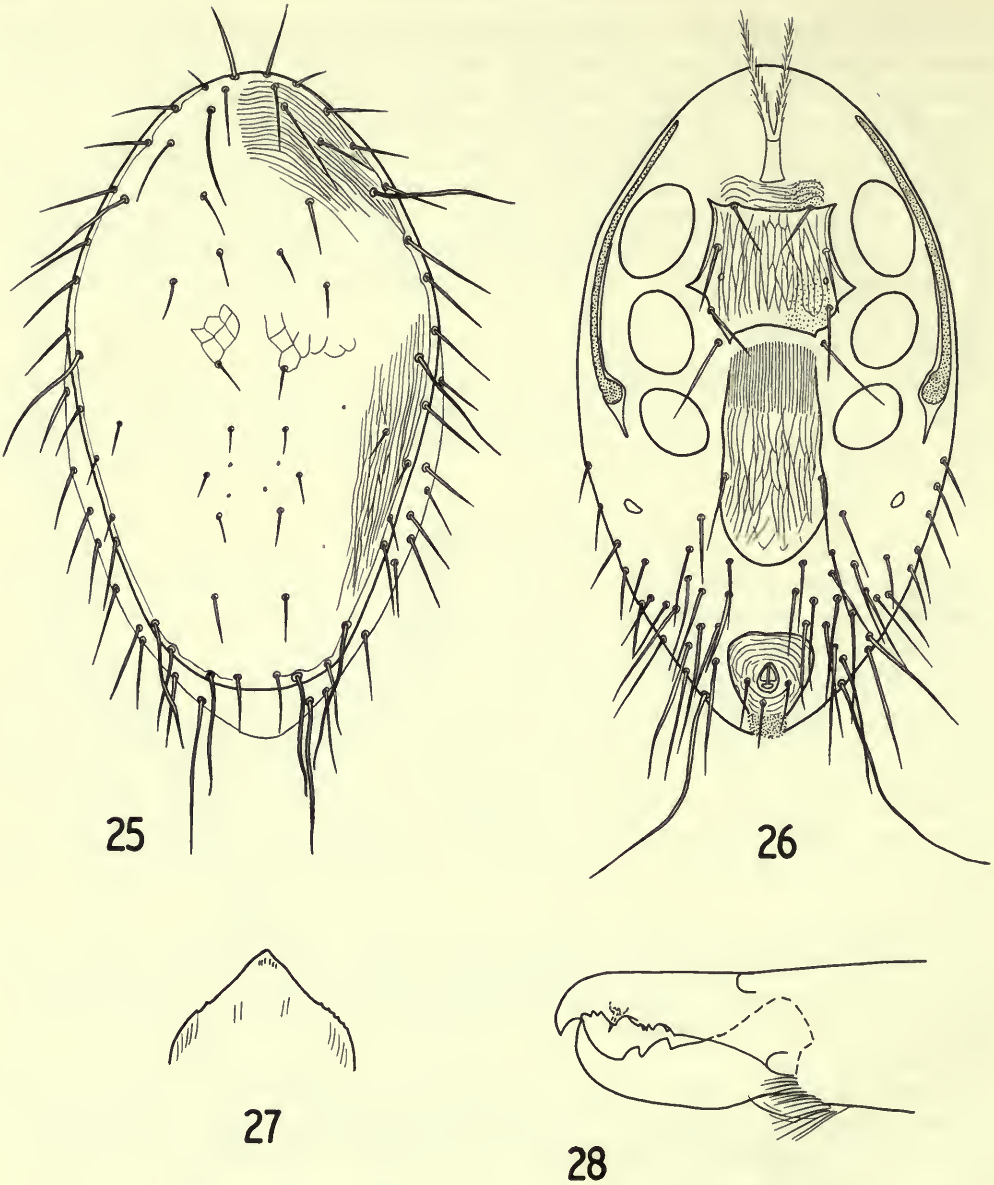
All setae on leg I simple. Tarsus II with five, tarsus III with three and tibia with two, tarsus IV with five, tibia with two and genu with one, ventral spines or stout setae. Remaining setae simple. All legs with a pulvillus and two claws.

MALE : Unknown.

LOCALITY : The holotype female (1963.10.3.91) and one paratype (1963.10.3.92) from *Dynastes* sp. (Col., Dynastidae) (2860), Caracas, August 1957.

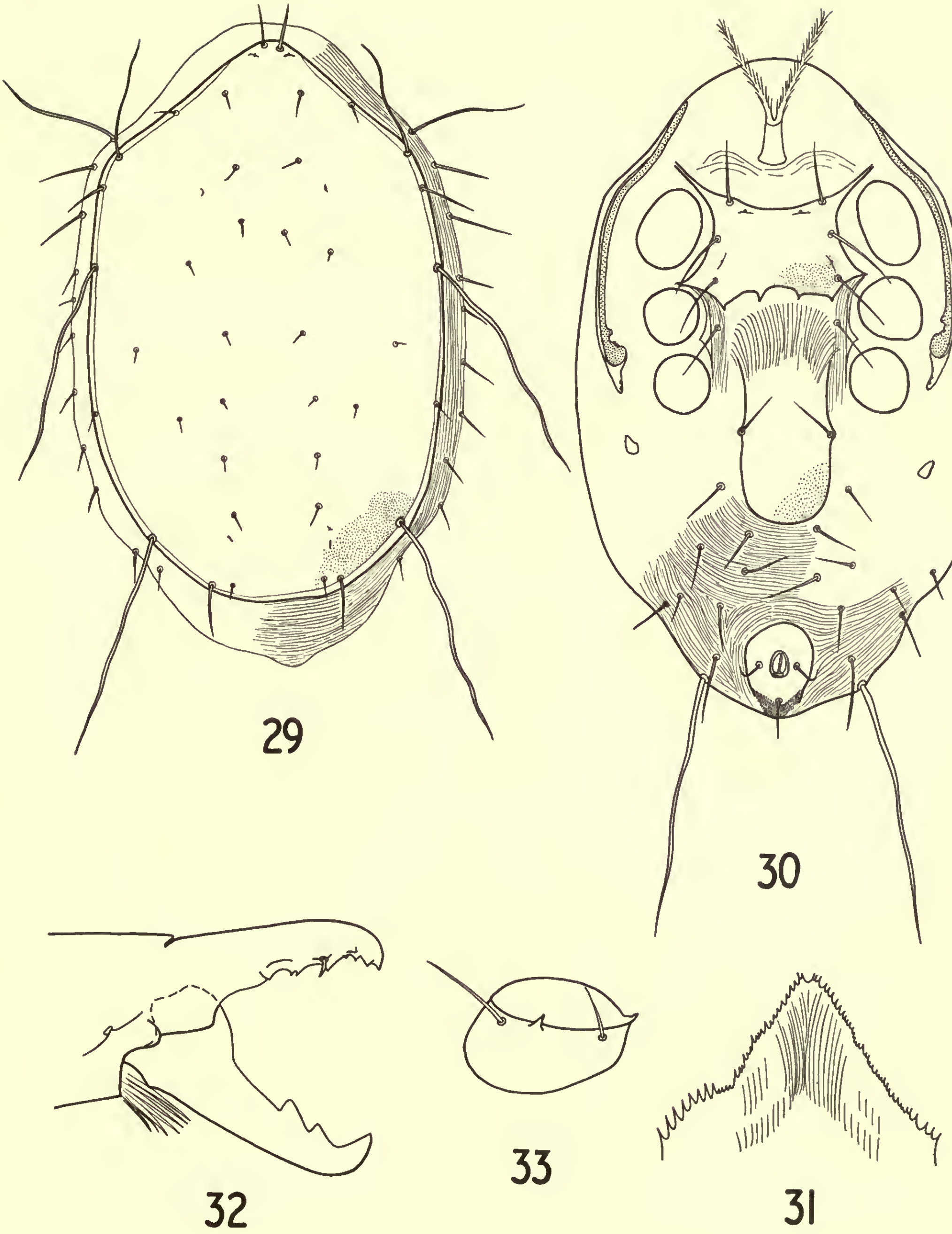
" *Coleolaelaps* " *granulatus* sp. nov.

FEMALE : Dorsal shield (805–837μ long × 540–581μ wide) finely granular and bearing 19 pairs of setae, the shortest being about 20μ and the longest about 380μ (Text-fig. 29).



Figs. 25–28. *Coleolaelaps striatus* sp. nov., female. Fig. 25 dorsum. Fig. 26 venter. Fig. 27 tectum. Fig. 28 chelicera.

Tritosternum normal, with pilose laciniae. Pre-endopodal area weakly sclerotized. Sternal shield shallow, granulate, weakly sclerotized, and with posterior margin irregular. Sternal setae long (Text-fig. 30). Metasternal and genital setae shorter than sternal setae. Genital shield weakly sclerotized, granulate. Anal shield ovoid, without ornamentation. Peritreme extending to the middle of coxa I ;



FIGS. 29–33. " *Coleolaelaps* " *granulatus* sp. nov., female. Fig. 29 dorsum. Fig. 30 venter. Fig. 31 tectum. Fig. 32 chelicera. Fig. 33 coxa II.

peritrematal shield tapering a little beyond the stigma. Metapodal shields very small. Membrane posterior to the genital shield with about nine pairs of setae.

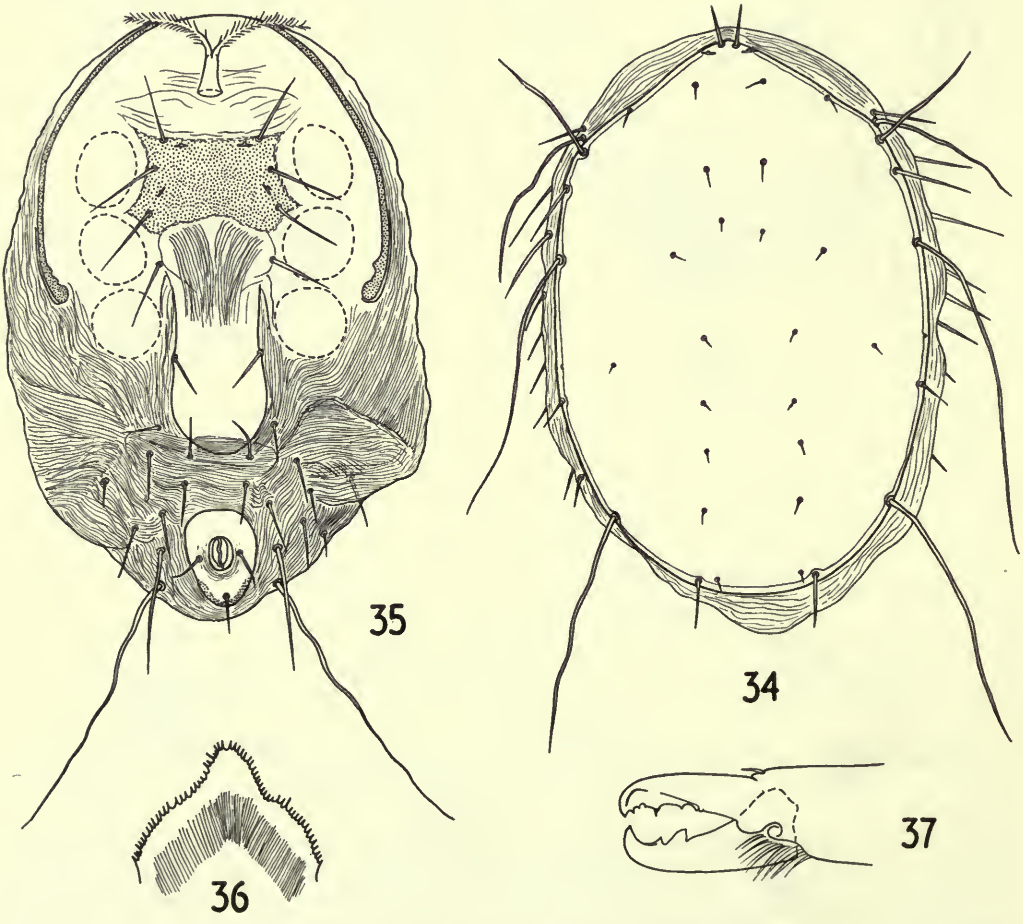
Corniculi long and slender. Internal posterior rostrals longest of gnathosomal setae. Chaetotaxy of pedipalp simple ; apotele with two prongs. Tectum entirely denticulate (Text-fig. 31). Fixed digit of chelicera with one large and about six small teeth ; movable digit with two large teeth (Text-fig. 32).

All setae on legs simple. Tarsus I with claws markedly reduced ; tarsi II–IV with well developed claws. Legs II–IV with some stout setae. Coxae II with a small anteriorly-projecting spur (Text-fig. 33).

MALE : Unknown.

LOCALITY : The holotype female (1963.10.3.93) and one paratype (1963.10.3.94) from a scarabaeid beetle (2684), Río Caura, Bolívar, Venezuela, May 1957.

This and the following species differ mainly from typical *Coleolaelaps* in the



FIGS. 34–37. " *Coleolaelaps* " *latisternalis* sp. nov., female. Fig. 34 dorsum. Fig. 35 venter. Fig. 36 tectum. Fig. 37 chelicera.

complete reduction of the claws on leg I and in the reduction in number of the dorsal setae. It may well prove necessary, when more material has been examined, to propose new taxa for the reception of these species.

"Coleolaelaps" latisternalis sp. nov.

FEMALE : Dorsal shield (795–826μ long × 518–591μ wide) finely granular, devoid of any ornamentation, and bearing 18 pairs of simple setae of which 11 pairs are extremely short (*c.* 25μ) and the longest pair is up to 450μ (Text-fig. 34).

Tritosternum well developed with pilose laciniae. Pre-endopodal shields almost non-existent, discernible only as faint marks on the membrane. Sternal shield broad, granular, weakly sclerotized, and bearing three pairs of long setae (Text-fig. 39). Metasternal setae situated on the membrane. Genital shield without ornamentation, setae simple. Anal shield also without ornamentation and bearing three simple setae. Peritreme extending to the middle of coxa I. Peritrematal shield very narrow, scarcely noticeable, not extending posterior to the stigma. Metapodal plates apparently absent. Membrane posterior to the genital shield with about nine pairs of setae, of which one pair is extremely long (*c.* 450μ).

Corniculi long and slender. Internal posterior rostrals longer than other gnathosomal setae. Chaetotaxy of pedipalps simple ; apotele with two prongs. Tectum (Text-fig. 36) finely denticulate along its outer margin. Fixed digit of chelicera with six small teeth and one large ; movable digit with two large teeth (Text-fig. 37).

Claws on leg I markedly reduced ; legs II–IV with well developed claws. Chaetotaxy of legs simple.

MALE : Unknown.

LOCALITY : The holotype female (1963.10.3.95) and 22 paratypes (1963.10.3.96–105) from a scarabaeid beetle (2685), Río Caura, Bolívar, May 1957.

FAMILY DIARTHROPHALLIDAE

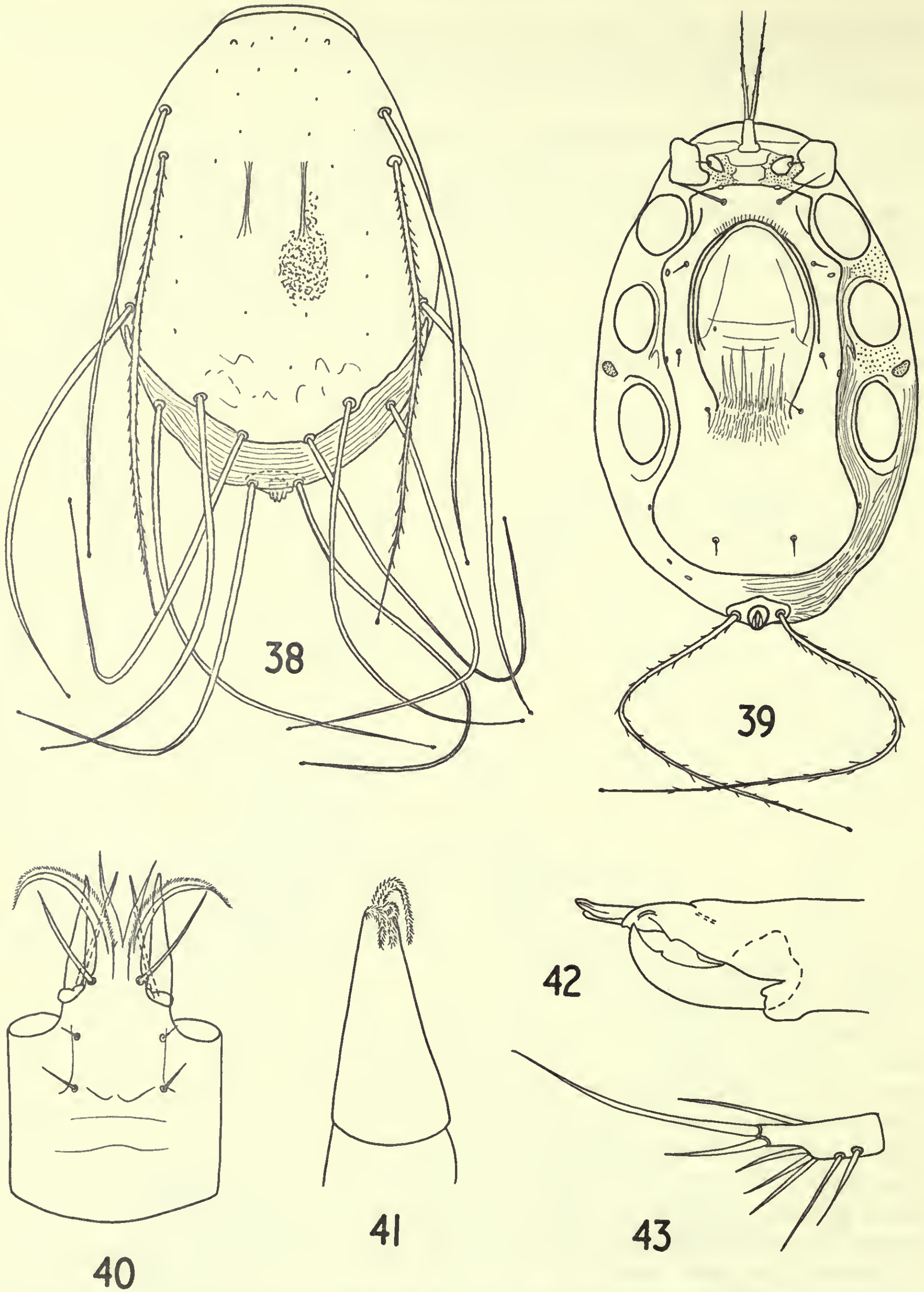
Genus **BRACHYTREMELLA** Trägårdh

Brachytremella womersleyi sp. nov.

FEMALE : Dorsal shield (430μ long × 291μ wide) smooth and weakly sclerotized ; bearing five pairs of long stout pilose setae (up to 460μ) and a number of extremely minute setae (Text-fig. 38).

Tritosternum with a short base and slender, barely pilose, laciniae. Presternal setae on discrete platelets. As in other members of the Diarthrophallidae the sterniti-genital shield extends almost to the anal shield. The epigynial shield is large and tongue shaped and is not articulated at the base (Text-fig. 39). Sternal setae I are three times the length of sternal setae II–IV. A further pair of short setae is situated near the posterior margin of the sterniti-genital shield. The anal shield is small and bears (as appears throughout the family) a pair of stout long paranal setae, and no postanal seta. Stigma and peritreme typical of the family.

Corniculi long and slender ; the tips curving outwards a little (Text-fig. 40). Rostral setae very long ; posterior rostrals very short and represented by only one pair, the internals being absent. Capitular setae short also. Femur of pedipalp



Figs. 38–43. *Brachytremella womersleyi* sp. nov., female. Fig. 38 dorsum. Fig. 39 venter. Fig. 40 venter of gnathosoma. Fig. 41 tectum. Fig. 42 chelicera. Fig. 43 tarsus I.

with a long pilose seta dorsally ; tibia with two long slender setae distally, and tarsus with one long seta. Remaining chaetotaxy consisting of short fine setae. Tectum with three laciniate digits (Text-fig. 41). Chelicera as in Text-figure 42.

Leg I 177μ long. Tarsus I without ambulacrum (Text-fig. 43), but with a long terminal seta ; genu with one long pilose lateral seta ; femur with one long dorsal seta ; remaining setae on legs simple. Leg II 233μ long. Femur with a long pilose seta distally ; remaining setae simple. Ambulacrum without claws. Leg III 240μ long. Femur and genu each with a long pilose seta distally ; remaining setae simple ; ambulacrum without claws. Leg IV 240μ long, similar to leg III.

LOCALITY : A single female (1963.10.3.106) from *Passalus flascala* (Col., Passalidae) (1387), Pie del Cerro, January 1956.

The family Diarthrophallidae has been discussed in detail recently by Womersley (1961, 1961a) and his concept of *Brachytremella* is followed.

FAMILY HOPLOMEGISTIDAE

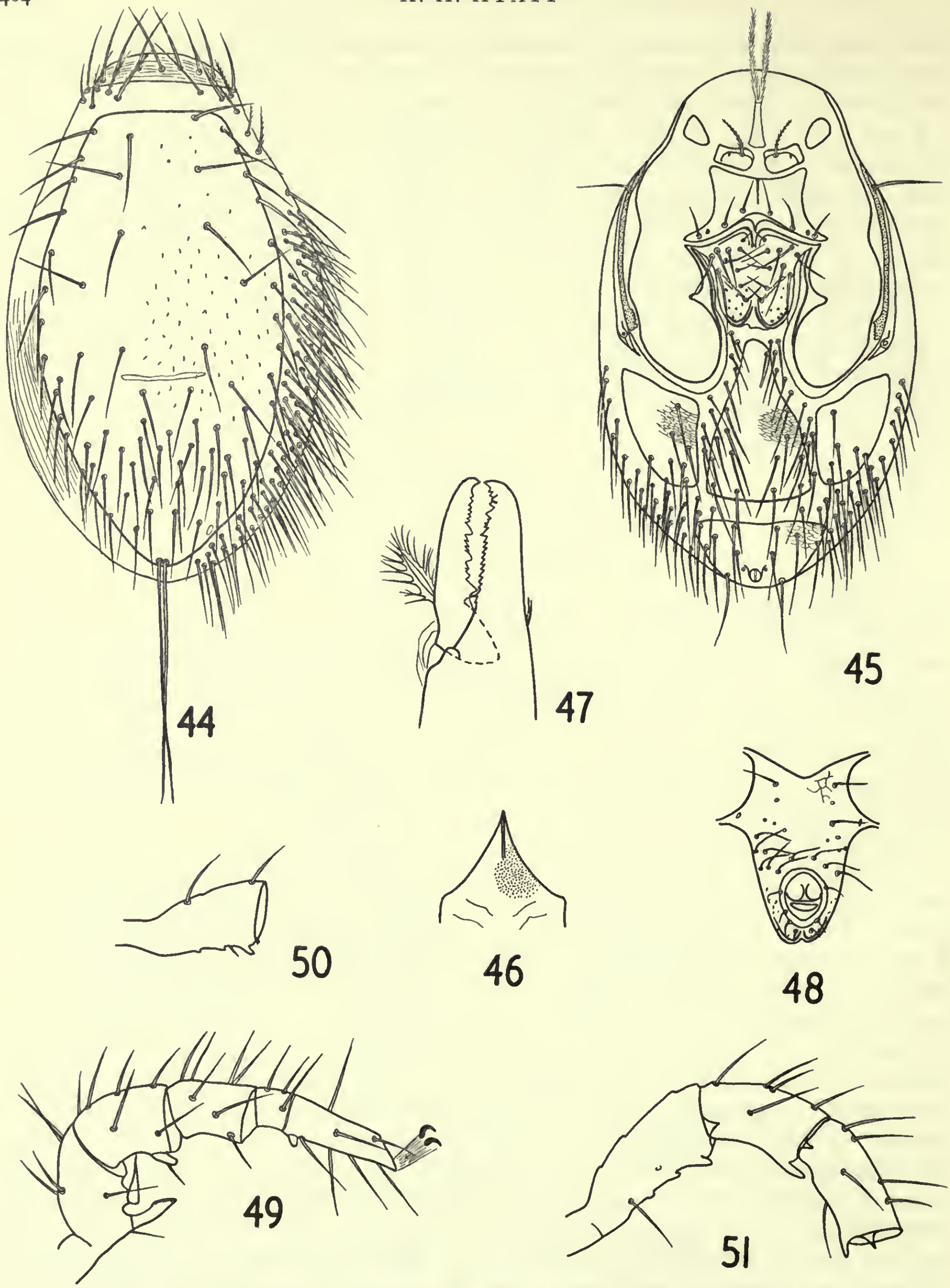
Genus ***HOPLOMEGISTUS*** Berlese

Hoplomegistus bicrinus Berlese

Hoplomegistus bicrinus Berlese, A. 1918. Redia **13** : 142.

FEMALE : Dorsal shield (1,260μ–1,290μ long × 640–693μ wide) densely granular, and bearing about 36 pairs of simple setae of which one pair on the posterior border of the shield has the bases touching and are about 480μ long (Text-fig. 44). The dorsal shield bears also numbers of distinct pores. Anterior to the dorsal shield, and separated from it by membrane, is a narrow sclerotized strip bearing seven setae. The membrane surrounding the dorsal shield bears a large number of simple setae as shown in the figure. In some specimens the interscutal membrane is sclerotized and forms an extension of the dorsal shield.

Tritosternum with a narrow base and pilose laciniae. Jugularia well sclerotized ; setae long and bipectinate. Sternal shield narrowest in the middle and bearing three pairs of simple setae along its concave posterior margin (Text-fig. 45). Latigynial shield fused medially and bearing ten pairs of setae. The most anterior pair is very short. These are followed by a posterior row of four pairs of long setae, and posterolaterally a further two pairs of long setae. Medially are three pairs of short setae. The pore-field in the posterior half of the latigynial shield is clearly divided into two areas. The ventral shield is roughly triangular, rounded anteriorly, and slightly convex posteriorly. It bears about seven pairs of simple setae and is flanked by about 12 pairs of setae, although neither those on the shield, nor on the surrounding membrane, are arranged symmetrically. Ventri-anal shield broader than long (*c.* 280μ × 290μ) and with about six pairs of setae. Lying along the posterior margin of the ventri-anal shield is a pair of platelets (not shown in Text-fig. 45) each bearing a single seta. Endopodal shields surrounding coxae III and fused with the peritrematal shield. Stigma between coxae III and IV ; peritreme extending to coxa I ; peritrematal shield with a strong seta opposite coxa II.



FIGS. 44–51. *Hoplomegistus bicrinus* Berlese. Fig. 44 dorsum of female. Fig. 45 venter of female. Fig. 46 tectum of female. Fig. 47 chelicera of female. Fig. 48 sternitigenital shield of male. Fig. 49 leg II of male. Fig. 50 femur III of male. Fig. 51 leg IV of male.

Corniculi pointed, noticeably horn-like in appearance. Gnathosomal setae long, arranged almost in a straight line. Majority of pedipalpal setae simple, remainder finely pilose on one or both margins. Apotele with two slender prongs. Tectum (Text-fig. 46) a sclerotized triangular plate. Fixed digit of chelicera with a large basal tooth and about 22 smaller teeth ; movable digit with three large teeth and 11 small teeth (Text-fig. 47).

Leg I 1,601µ long, without ambulacrum ; all setae fine although some pilose. Legs II–IV with a pulvillus and two claws ; all setae simple. Tarsus IV with a long seta distally. Leg II 1,240µ long, leg III 1,340µ, leg IV 1,810µ.

MALE : Dorsal shield (1,350–1,728µ long × 795–983µ wide) similar in structure and chaetotaxy to the female. As in the female, the interscutal membrane in some specimens is sclerotized.

The sterniti-genital shield (Text-fig. 48) bears at least a dozen pairs of setae, although as they are not arranged symmetrically, and some are broken off in all the specimens examined, it is not possible to be sure of the exact number present. The remaining sclerotization and chaetotaxy of the venter are similar to that of the female.

Venter of gnathosoma, tectum, chelicerae, and chaetotaxy of pedipalp as in the female.

Leg I very slender ; setae fine, some pilose. Leg II (Text-fig. 49) with two ventral spurs on the femur, one on the genu, and one on the tarsus. A small ventral spur and two small excrescences on the femur are the only noticeable armature on leg III (Text-fig. 50). There is, however, in addition to the normal simple chaetotaxy, a long erect seta on genu III. On leg IV the tarsus is unarmed, but the tibia has one ventral and one lateral spur at its distal end, and the genu is similarly armed, whilst the femur is similar to that of leg III, having a spur and two small excrescences ventrally (Text-fig. 51). The chaetotaxy of legs II–IV is simple. Tarsus IV has three long erect setae dorsally. Legs II–IV with a pulvillus and two claws.

The specimens examined (15 ♂♂ and 37 ♀♀) show considerable variation in the degree of sclerotization of the interscutal membranes, both dorsal and ventral, in the amount of reticulation of the ventral shields (completely lacking in some specimens), and in the arrangement and lengths of setae on the ventral shields. The figures given of the dorsum (Text-fig. 44) and venter (Text-fig. 45) are fairly typical.

DISTRIBUTION : Berlese (1918) was unable to give a locality for *H. bicrinus* (" *Habitat ubi?* "), and since that date this species has not appeared in the literature. The present collection from Venezuela includes the following specimens : nine males and 22 females from *Passalus flascala* Perch (Col., Passalidae) (1387), Pie del Cerro, January 1956 ; one male from *Passalus ? flascala* (1384), Los Chorros, January 1956 ; one male from *Passalus ? flascala* (2258), Copey, September 1956 ; one male and three females from a passalid beetle (2329), Mérida, 3 December 1956 ; two males and three females from a passalid (2675), Río Caura, Bolívar, May 1957 ; one male from a passalid (2932), Cabure, 14 December 1957 ; and nine females from passalids (3256 and 3259), San Juan de Manapiare, Amazonas, April 1958.

For the present, the specimens from Venezuela are identified with *Hoplomegistus bicrinus* Berlese, 1918, as they compare very favourably with Berlese's description, especially in the presence of the two long setae situated medially at the posterior of the dorsal shield, and in the armature of the legs. Several other related species, e.g. *Megisthanus balzani* Canestrini, 1896 (figured by Canestrini, 1897) ; *Hoplomegistus armiger* Berlese, 1888 (figs.) and figured subsequently by Stoll (1892) and Turk (1948) ; and *Hoplomegistus trapeziger* Berlese, 1910 ; and *Hoplomegistus tragardhi* Baker & Wharton, 1952, are neither described nor figured in enough detail to be absolutely sure of their identity. When a detailed revision can be made of the Hoplomegistidae and Megisthanidae it may be found that a number of the described species of these large and conspicuous mites can be synonymized.

Family Diplogyniidae

Genus ***TRICHODIPLOGYNIUM*** Trägårdh

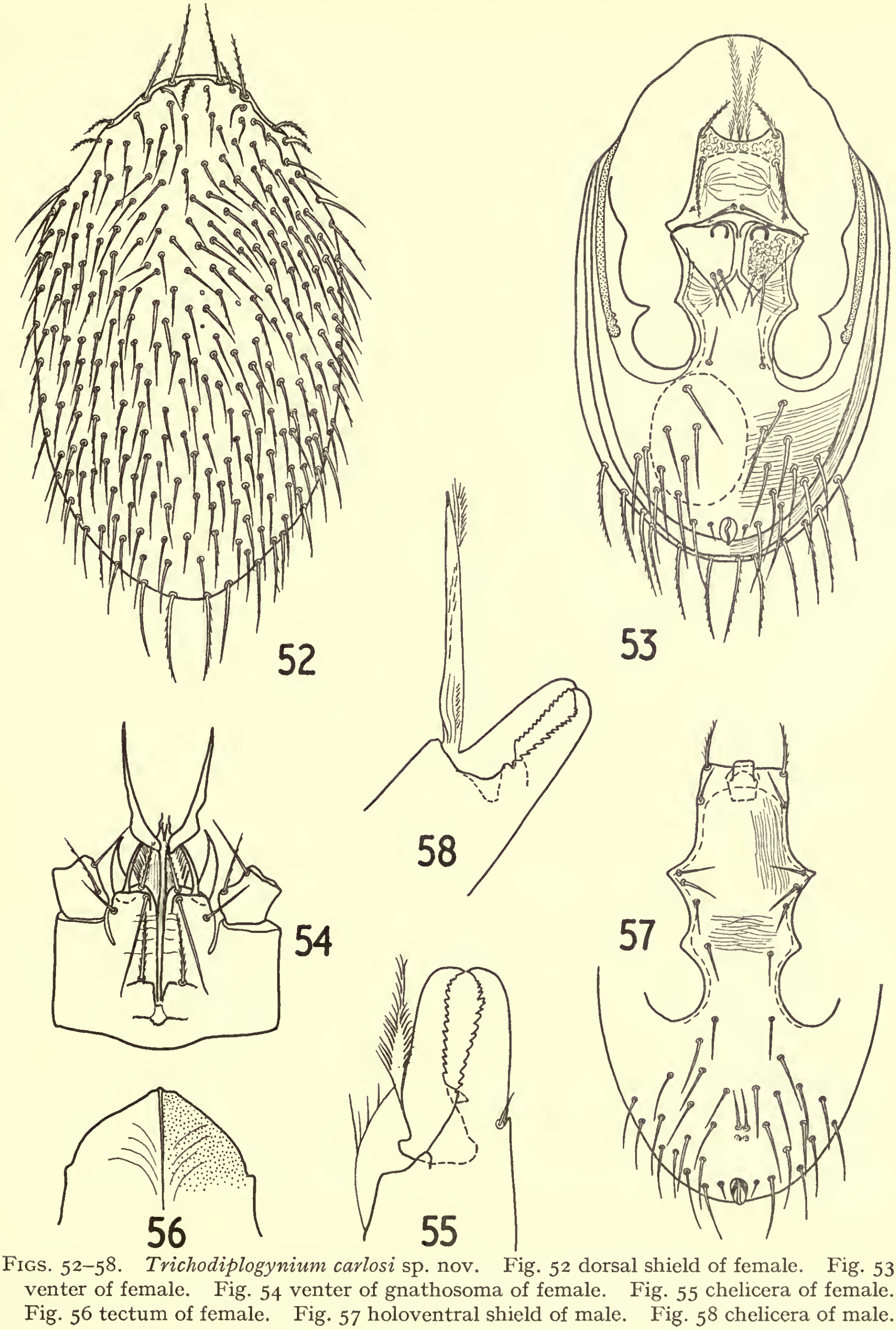
Trichodiplogynium carlosi sp. nov.

Female : Dorsal shield (743–764μ long × 446–488μ wide) bearing about 270 setae not entirely arranged symmetrically (Text-fig. 52). Two vertical pairs are slightly pilose and directed anteriorly. A number of the other setae also show slight pilosity. The marginal setae increase in length progressively towards the posterior.

Base of tritosternum greatly reduced ; the two laciniae very fine and pilose. Sternal shield broad, parallel sided, widening posteriorly, concave and heavily sclerotized anteriorly, and bearing three pairs of setae of which the anterior two pairs are finely pilose and the median posterior pair simple (Text-fig. 53). The lyriform lateral shields bear two pairs of setae situated close together and near the posterior margin. The fused ventral and anal shields cover the entire ventral area posterior to the genital region, with the exception of the surrounding strip of membrane and the underlying margin of the dorsal shield. The endopodal shields appear as a thickened border to the ventral shields. The chaetotaxy of the ventro-anal area comprises one pair of setae between coxae IV, ten pairs of long setae posterior to coxae IV, and a pair of very short setae lateral to the anus. Post-anal seta absent. Stigma situated opposite the anterior part of coxa IV, and peritreme extending anteriorly to the level of coxa I.

Venter of gnathosoma shown in Text-figure 54. Corniculi long and incurved. Rostral, external posterior rostral and capitular setae faintly pilose. Internal posterior rostrals situated close to rostrals and about twice as long as the other setae. Chaetotaxy of pedipalp simple ; setae on femur and genu long. Apotele two pronged. Fixed digit of chelicera with about 16 small teeth ; movable digit with one large basal tooth and about 14 small teeth (Text-fig. 55). Tectum as in Text-figure 56.

Leg I 930μ long, slender, though noticeably swollen in its distal half. Majority of setae long and fine ; some pilose. Legs II–IV with a pulvillus and two claws. Chaetotaxy comprising slender setae only with some slightly pilose. Tarsus IV has a long basal seta dorsally.



FIGS. 52–58. *Trichodiplogynium carlosi* sp. nov. Fig. 52 dorsal shield of female. Fig. 53 venter of female. Fig. 54 venter of gnathosoma of female. Fig. 55 chelicera of female. Fig. 56 tectum of female. Fig. 57 holoventral shield of male. Fig. 58 chelicera of male.

MALE : Dorsal shield (743–848μ long × 435–507μ wide) very similar to the female. The ventral and anal shields are fused to form the holoventral shield (Text-fig. 57) which covers the entire venter, except for the narrow surrounding membrane and the underlying margin of the dorsal shield as in the female. The intercoxal region bears seven pairs of setae of which sternal setae I are finely pilose. Posterior to coxae IV are 11–16 pairs of setae (excluding the anal setae) of which one central pair has the bases contiguous. The endopodal shields appear as a thickened border to the ventral shield.

Venter of gnathosoma similar to female, but internal posterior rostral setae equal in length to other rostral setae. Tectum and pedipalp as in the female. Dentition of chelicerae similar to the female, but synarthrodial brush twice as long as the movable digit (Text-fig. 58).

Leg I 910μ long. Chaetotaxy of legs simple as in the female. Tarsus IV apparently lacking the long dorsal seta of the female.

LOCALITY : The holotype female (1963.10.3.130), allotype male (1963.10.3.131), and 27 male and 33 female paratypes (1963.10.3.132–141) from a passalid beetle (2651), Río Caura, Bolívar, May 1957.

Hitherto only four species of the genus have been described ; all by Trägårdh (1950). Two, *bipilis* and *surinamense* are known only from the female ; *sahlbergi* is known only from the male ; and *hirsutum* is known from both sexes. The female of the present species bears two pairs of setae on the lateral shields as in *bipilis*, but they are situated on the posterior borders of the shields and not one each anteriorly and posteriorly as in that species. The male of the present species is closest to *sahlbergi* in that the synarthrodial brush is twice as long as the movable digit, but the ventri-anal area bears only seven pairs of setae as opposed to about 30 pairs in *sahlbergi*. *T. carlosi* bears about 260 pairs of dorsal setae whereas all of Trägårdh's species bear in the region of 300 pairs of setae.

This new species of *Trichodiplogynium* is dedicated to Dr. Carlos Díaz-Ungría.

Genus ***HETERODIPLOGYNIUM*** Trägårdh

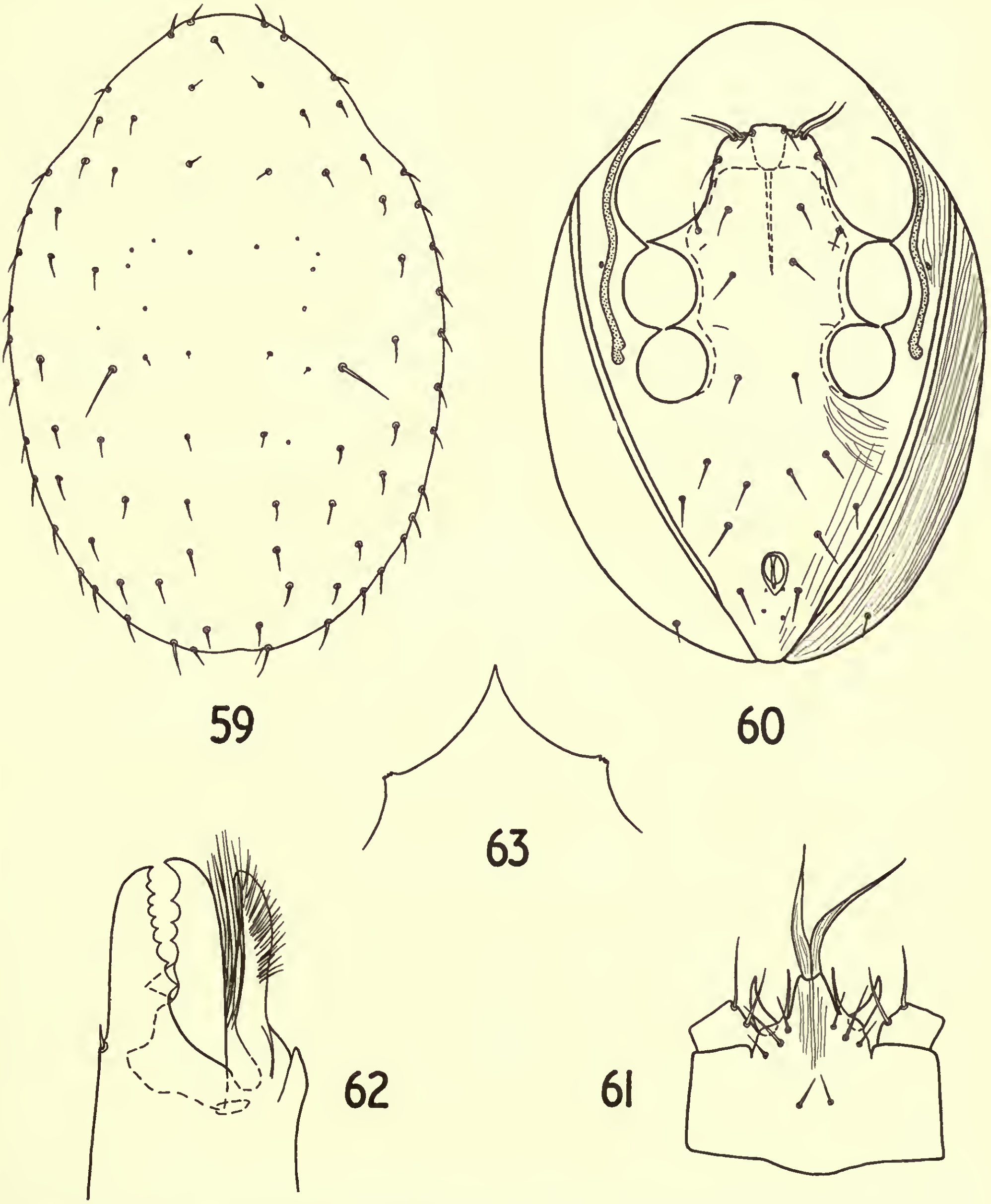
Trägårdh (1950) erected the genus *Heterodiplogynium* and proposed also a new subfamily, Heterodiplogyniinae, on the characters of a new species, *vestitum*, which differed from other diplogyniids in having along each side of the idiosoma a narrow sclerotized band clothed with small spinulae, and in possessing two groups of porose areas to the side of each peritreme.

The present collection contains a single male which appears to be congeneric with Trägårdh's species in the structure of the ventral shields, chelicerae, and gnathosoma, but certainly lacks the minute spinulae of *vestitum*. It possesses the *areae porosae* of *vestitum*, but so also, apparently, do most other diplogyniids! Therefore I consider Trägårdh's erection of a new subfamily for *Heterodiplogynium vestitum* to be quite unjustified.

Heterodiplogynium secundum sp. nov.

MALE : Dorsal shield (518μ long × 371μ wide) without ornamentation. The chaetotaxy comprises only simple setae. The majority of the setae are from

15–25μ long, and 14–15 pairs are situated on the margin of the shield posterior to the "shoulders". One pair only, just posterior to the centre of the shield, is 35μ long. The central area of the dorsal shield bears only pores and a few minute setae (Text-fig. 59).



Figs. 59–63. *Heterodiplogynium secunda* sp. nov., male. Fig. 59 dorsal shield. Fig. 60 venter. Fig. 61 venter of gnathosoma. Fig. 62 chelicera. Fig. 63 tectum.

The chaetotaxy of all the ventral shields is similar to that of *H. vestitum* Trägårdh. The sterniti-genital shield bears at its anterior margin one pair of short setae at the corners of the genital orifice and two pairs of closely-set long setae (Text-fig. 60). The remainder of the sterniti-genital region bears four pairs of setae and the ventri-anal area bears six pairs. The marginal shields bear one pair of short setae posteriorly. The stigma is situated opposite the centre of coxa IV, and the narrow granular peritreme extends anteriorly to the edge of the gnathosoma.

Venter of gnathosoma shown in Text-figure 61. Its structure is very similar to that of *H. vestitum* : the three rostral setae are arranged in an oblique straight line, and the centre one (the internal posterior rostral) is the longest. The capitular seta is simple. Corniculi curved but not pointed. Apart from three stout pilose setae on the palpfemur, all setae on the palp are simple and slender. Apotele two pronged. Fixed digit of chelicera with eight small teeth ; movable digit with one large basal tooth and three smaller ones. Arising from the base of the movable digit are two appendages, one finger shaped and strong, and the other laciniate (Text-fig. 62). The tectum is shown in Text-figure 63.

Leg I (354µ long) with some of the stouter setae pilose ; remainder simple. Legs II–IV with a pulvillus and two claws and having simple chaetotaxy : a few of the setae are slightly pilose.

LOCALITY : A single male (1963.10.3.142) from a passalid beetle (2496) at Río Caura, Bolívar, May 1957.

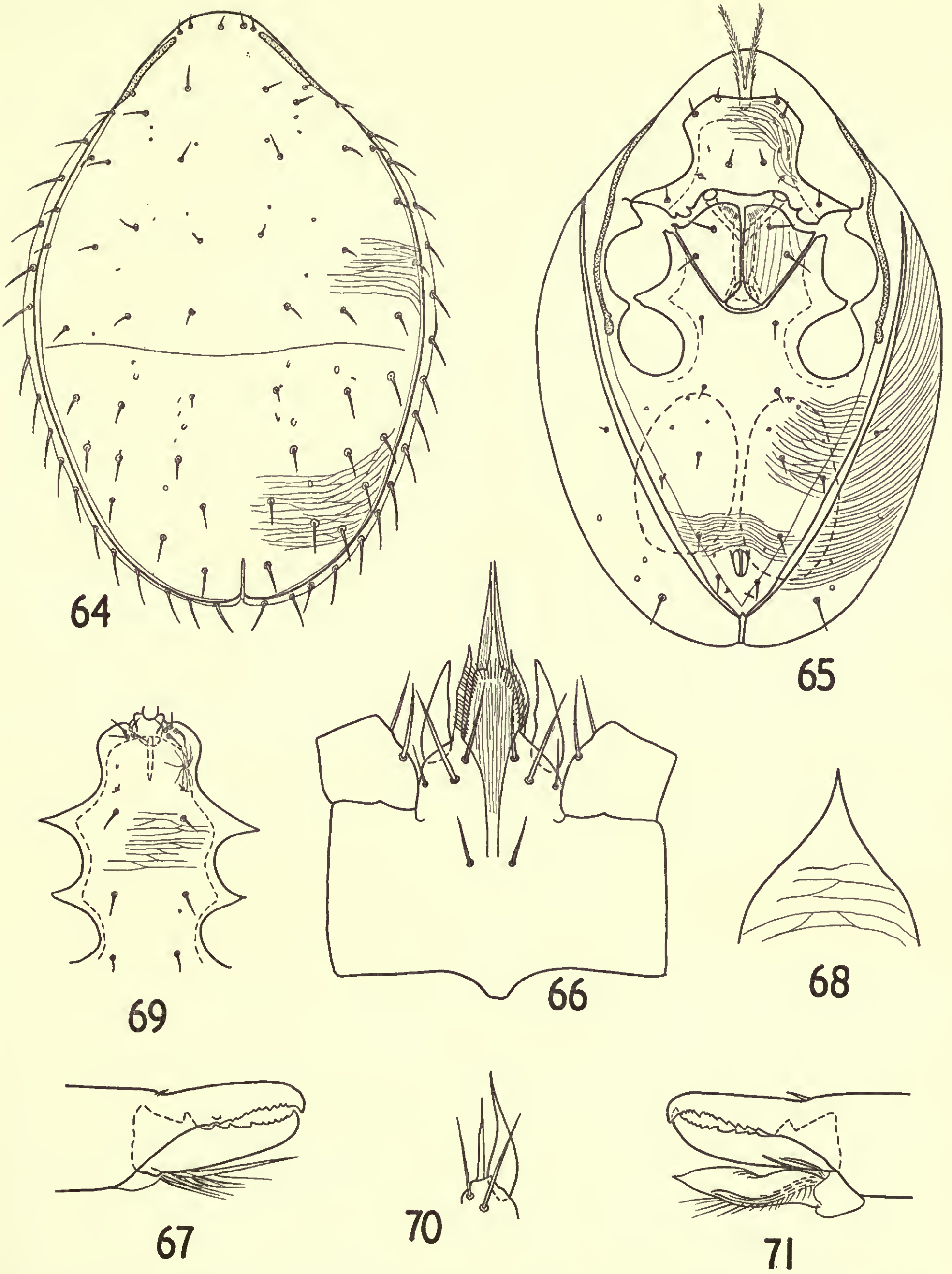
Genus ***BRACHYSTERNUM*** Trägårdh

Brachysternum espinosai sp. nov.

FEMALE : Dorsal shield (890–900µ long × 620µ wide) with 27 pairs of rather short simple setae and one unpaired seta posterior to the verticals. Marginal shields with 16 pairs of longer and stouter setae. Ornamentation comprising very faint reticulations and a distinct but faint transverse dividing line medially. Posterior margin of dorsal shield deeply incised (Text-fig. 64).

Tritosternum with a narrow base and pilose laciniae. Sternal and metasternal shields fused to form a single shield. Sternal setae I and II close together and situated obliquely at the antero-lateral margin of the shield. Setae III situated about two-thirds of the way down the centre of the shield. Sternal setae IV (the metasternals) situated on the postero-lateral extensions of the sternal shield (Text-fig. 65). Lateral shields longitudinally striated, and each bearing two pairs of simple setae in its anterior half. The ventral shield tapers sharply to a point posterior to the anus where the marginal shields meet also. Ventral shields with six pairs of short simple setae. Ventral portions of marginal shields with two pairs of setae. Peritreme extending anteriorly to beyond coxa I. All ventral shields ornamented with fine close striations and reticulations.

Venter of gnathosoma shown in Text-figure 66. All gnathosomal setae simple ; rostrals and internal posterior rostrals twice as long as external posterior rostrals and capitulars. Corniculi broad and tapering with a distinct swelling along the internal margins. Chaetotaxy of pedipalp simple. Apotele with two prongs.



FIGS. 64–71. *Brachysternum espinosai* sp. nov. Fig. 64 dorsum of female. Fig. 65 venter of female. Fig. 66 venter of gnathosoma of female. Fig. 67 chelicera of female. Fig. 68 tectum of female. Fig. 69 intercoxal region of male. Fig. 70 corniculus of male. Fig. 71 chelicera of male.

Fixed digit of chelicera with 11 small subequal teeth ; movable digit with one large basal tooth and eight irregularly-spaced small subequal teeth (Text-fig. 67). Tectum sharply pointed and with concave sides (Text-fig. 68).

Leg I (661µ long) without ambulacrum. Chaetotaxy comprising simple setae only ; longest on the tarsus and becoming shorter progressively towards the coxa. Legs II–IV with a pulvillus and two claws ; all setae simple.

MALE : Dorsal shield (859µ long × 591µ wide) apparently the same as the female. Intercoxal region shown in Text-fig. 69. Situated on each side of the genital opening is a cluster of four short simple setae. Remainder of intercoxal region with three pairs of setae. Ventral shield posterior to coxae IV with four pairs of setae. Ventral portion of marginal shields with two pairs of setae.

Venter of gnathosoma and pedipalps similar in structure to the female. Corniculi with a similar median swelling, tapering finely distally (Text-fig. 70). Fixed digit of chelicera with about 14 small subequal teeth ; movable digit with one large basal tooth and nine small irregularly-spaced teeth. A broad membraneous appendage arises from the base of the movable digit (Text-fig. 71). Tectum differing from the female in that the lateral margins are not concave, and the tip is rounded. Legs similar to the female.

LOCALITY : The holotype female (1963.10.3.143), allotype male (1963.10.3.144), and one male and nine female paratypes (1963.10.3.145–149) from *Hololepra humilis* (Col., Histeridae) (3207) ; and one paratype male (1963.10.3.150) from a passalid beetle (3256), San Juan de Manapiare, Amazonas, April 1958.

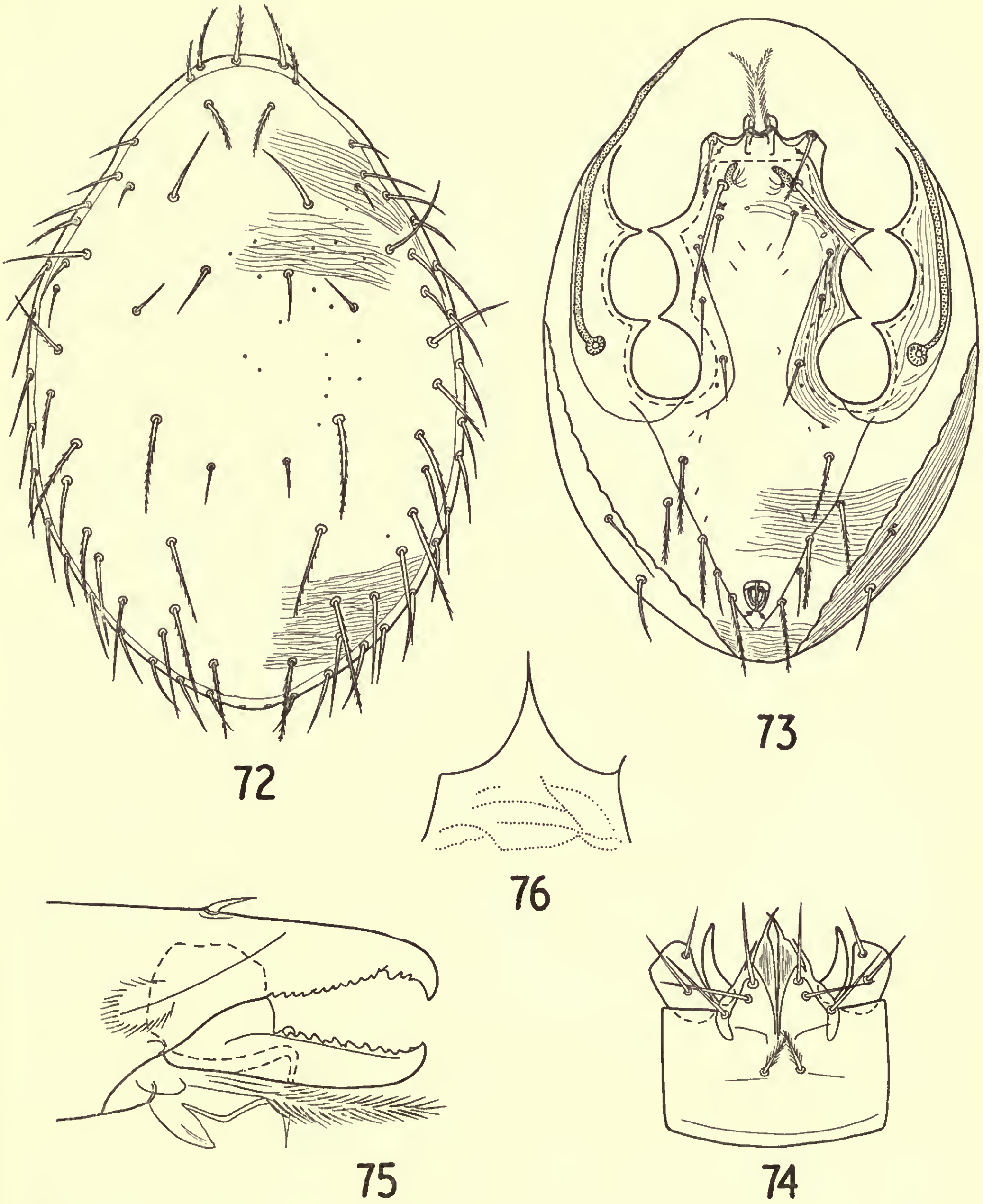
This species differs from the only previously-known representative of the genus, *Brachysternum acuminatum* Trägårdh, 1950, mainly in the chaetotaxy of the dorsal shield in both sexes, in the chaetotaxy of the intercoxal region of the male, and in the chaetotaxy of the venter of the gnathosoma.

Brachysternum espinosai is dedicated to Dr. Espinosa who assisted Dr. Díaz-Ungría during the collecting of the material upon which this paper is based.

Brachysternum cornutum sp. nov.

MALE : Dorsal shield (826µ long × 550µ wide) with 39 pairs of setae and one unpaired seta at the vertex. The majority of the setae are long (75–125µ) and a number of pairs are finely pilose. The entire shield is finely reticulated (Text-fig. 72).

Tritosternum with pilose laciniae. The sterniti-genital region is instantly distinguishable from that of *B. acuminatum* Trägårdh and *B. espinosai* sp. nov. although fundamentally it is of the same type as *acuminatum*. The genital orifice appears squarish with two lateral incurved flanges. The anterior margin of the sterniti-genital shield is markedly concave (Text-fig. 73). Sternal setae I reach posteriorly to the pore associated with the short setae III. Setae II long (115µ) and extremely broad : at their bases, below the surface, two horn-like processes are directed anteriorly. Setae III–VI are simple. The endopodal region is conspicuously striated. The remainder of the venter is similar to that of *acuminatum* : posterior to coxae IV are five pairs of setae of which four are of equal length and the fifth is shorter ; and the marginal shield bears two pairs of setae. The form of the stigma



FIGS. 72–76. *Brachysternum cornutum* sp. nov., male. Fig. 72 dorsum. Fig. 73 venter. Fig. 74 venter of gnathosoma. Fig. 75 chelicera. Fig. 76 tectum.

and peritreme are almost the same as in *acuminatum*. The whole ventral surface is finely reticulated.

The venter of the gnathosoma is shown in Text-figure 74. The three pairs of rostral setae are long and simple, whilst the capitular setae are short and bipectinate. The corniculi are strongly curved with finely rounded tips. Chaetotaxy of pedipalp normal ; apotele with two prongs. Fixed digit of chelicera with about 14 small subequal teeth and one larger tooth. Movable digit with about 12 subequal teeth. The synarthrodial membrane is slightly longer than the movable digit. Associated with the membrane is a hyaline appendage (Text-fig. 75). Tectum as in Text-figure 76.

Leg I 228μ long, slender and with simple chaetotaxy. Legs II–IV with pulvilli and two claws. Chaetotaxy essentially simple, a few setae pilose along one margin.

LOCALITY : A single male (1963.10.3.151) from a passalid beetle (2675), Río Caura, Bolívar, May 1957.

Genus ***TRIDIPLOGYNIUM*** Trägårdh

Tridiplogynium brenthi sp. nov.

FEMALE : Dorsal shield (661μ long × 507μ wide) broadly oval in outline. Vertical and post-vertical setae long and slender ; two pairs of dorsal and two pairs of posterior marginal setae long with finely-pilose extremities ; remainder of margin with 14 pairs of short setae, and the remainder of the dorsum with a number of very fine short setae and pores (Text-fig. 77).

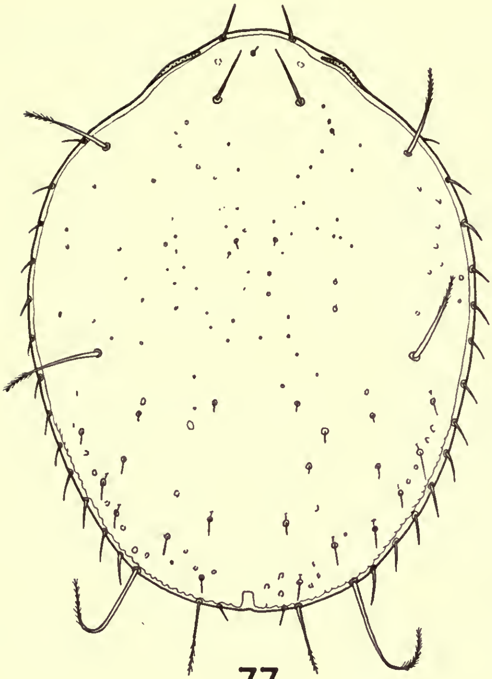
Tritosternum with a narrow base and pilose laciniae. Sternal shield strongly concave posteriorly and with long postero-lateral extensions, and bearing three pairs of setae (Text-fig. 78). Lateral shields with the three pairs of setae characteristic of the genus. The ventral shield extends almost to the posterior end of the idiosoma where it meets the junction of the broad ventral marginal shields. The ventral shield bears six pairs of setae posterior to the genital region, and the ventral marginal shields each bear at least one pair of setae. Peritreme extending anterior to coxa I. All ventral shields are striated.

Venter of gnathosoma as in Text-figure 79. Capitular setae short and pilose ; all rostral setae simple and longer. Corniculi tapering only in their distal thirds. Chaetotaxy of pedipalp simple ; apotele two pronged. Fixed digit of chelicera with ten subequal teeth ; movable digit with a large basal tooth and five smaller teeth. Movable digit with brush-like process just passing the tip of the digit (Text-fig. 80). Tectum pointed and with concave sides (Text-fig. 81).

Leg I 467μ long, with simple setae ; no ambulacrum. Legs II–IV each with a pulvillus and two claws. Femur II and genua III and IV each with a long distal seta dorsally (Text-fig. 82). Remaining chaetotaxy simple.

LOCALITY : A single female (1963.10.3.152) on *Brenthus championi* Sharp (Col., Brenthidae) (2868), Caracas, November 1957.

This species differs from the type of the genus, *T. inexpectatum* Trägårdh, mainly in the chaetotaxy of the dorsal shield, in the form of the gnathosoma, and in possessing a long erect seta on legs II–IV, although it is conceivable that these setae were missing in Trägårdh's single example.



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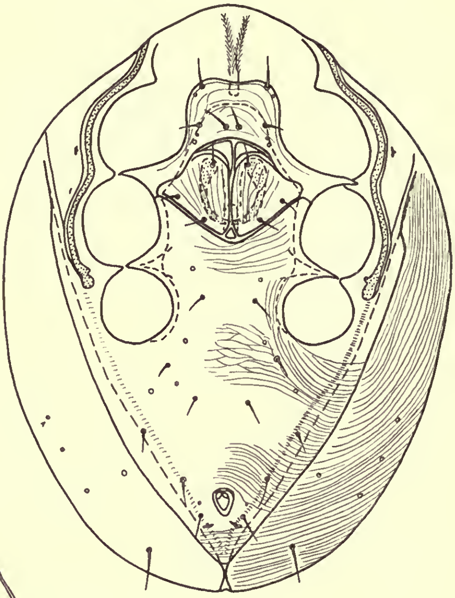

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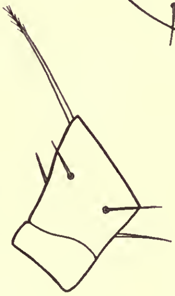

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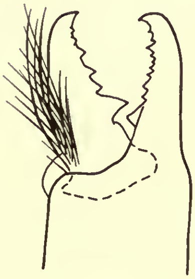

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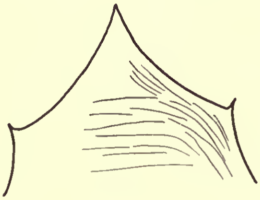

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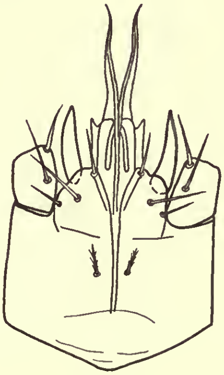

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FIGS. 77–82. *Tridiplogynium brenthi* sp. nov., female. Fig. 77 dorsal shield. Fig. 78 venter. Fig. 79 venter of gnathosoma. Fig. 80 chelicera. Fig. 81 tectum. Fig. 82 femur II.

Genus *CRYPTOMETASTERNUM* Trägårdh

Cryptometasternum diazungriai sp. nov.

FEMALE : Dorsal shield (540–591μ long × 310–371μ wide) without ornamentation; bearing 49 pairs of short simple setae and one unpaired seta at the vertex (Text-fig. 83).

Tritosternum narrow and delicate with finely-pilose laciniae. Sternal shield broadening out considerably posteriorly ; heavily sclerotized anterior and lateral margins. The three pairs of sternal setae are very short and fine : posterior pair near the centre of the posterior margin (Text-fig. 84). Metasternal setae very short. Lateral shields with two pairs of setae on the external margin. The ventral shield tapers sharply from the stigma to the anus and bears six pairs of simple setae. Stigma situated in line with the anterior part of coxa IV ; peritreme extending to the base of the gnathosoma.

Venter of gnathosoma shown in Text-figure 85. Capitular setae short and pilose ; other gnathosomal setae simple ; rostrals twice as long as posterior rostrals. Corniculi pointed. Chaetotaxy of pedipalp simple ; apotele two pronged. Fixed digit of chelicera with about 13 small subequal teeth, movable digit with one large basal tooth and about 15 small subequal teeth. Tectum as in Text-figure 86.

Leg I 498μ long, all setae simple, decreasing markedly in length from tarsus to trochanter. Legs II–IV with all setae short and simple ; ambulacra comprising a pulvillus and two claws.

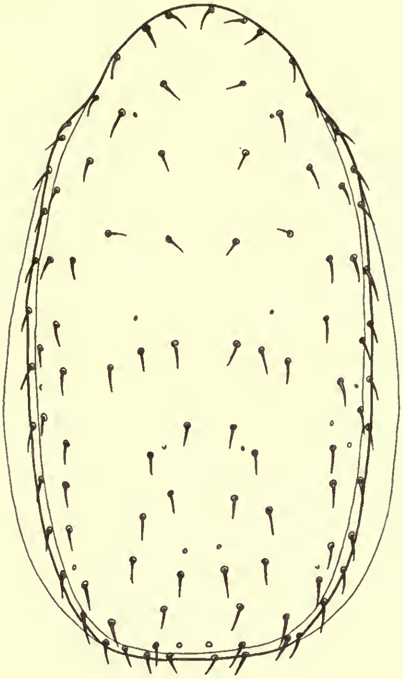
MALE : Dorsal shield (540μ long × 340μ wide) similar in structure and chaetotaxy to the female. Intercoxal region shown in Text-figure 87 ; setae short and fine. Region posterior to the stigma with six pairs of simple setae as in the female.

Gnathosoma and pedipalps similar in structure to the female. Corniculi shorter and blunter than in the female and not symmetrical. Fixed digit of chelicera with 12 subequal teeth ; movable digit with the large basal tooth and 13 subequal ones, and possessing a small appendage arising from the base of the digit (Text-fig. 88). Tectum similar to that of the female, but rounded anteriorly and less angular.

LOCALITY : The holotype female (1963.10.3.153), allotype male (1963.10.3.154), seven paratype females and five paratype males (1963.10.3.155–159) from *Dynastes* sp. (Col., Dynastidae) (2860), Caracas, August 1957.

The present species differs mainly from the three previously known members of the genus, *natalense* Trägårdh, 1950, and *derricki* and *queenslandense* Womersley, 1958, all keyed by Womersley (1958), in that the margins of the dorsal shield are not crenate as in *natalense* and *derricki*, and the dorsal shield bears 49 pairs of setae with none on the marginal shields, whereas in *queenslandense* the dorsal shield bears about 20 pairs, and the marginal shields seven or eight pairs.

FIGS. 83–88. *Cryptometasternum diazungriai* sp. nov. Fig. 83 dorsum of female. Fig. 84 venter of female. Fig. 85 venter of gnathosoma of female. Fig. 86 tectum of female. Fig. 87 intercoxal region of male. Fig. 88 chelicera of male.



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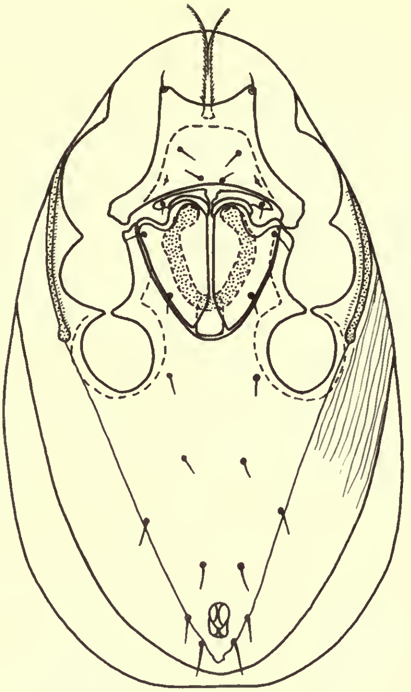

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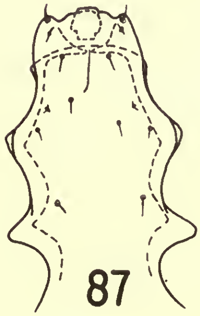

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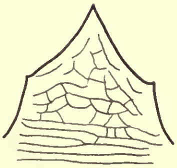

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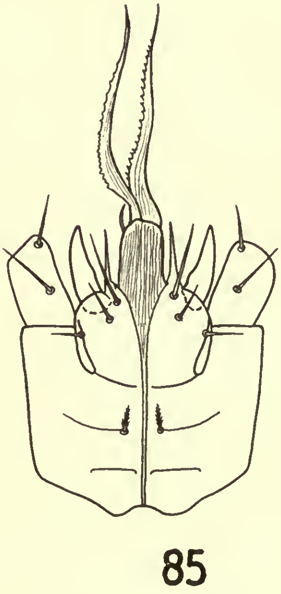

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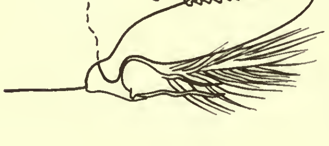


88

FAMILY EUZERCONIDAE

Genus ***EUZERCON*** Berlese

Euzercon balzani Berlese

Euzercon balzani Berlese, A. 1888. Bull. Soc. ent. Ital. **20** : 203.

FEMALE : Dorsal shield (1,013–1,392μ long × 775–983μ wide) heavily sclerotized and with fine reticulations around the entire margin (Text-fig. 89). The almost straight anterior margin bears two pairs of strong anteriorly projecting setae and a shorter unpaired seta, the latter usually to one side of the centre. Around each side of the dorsal shield are twelve strong setae up to 300μ in length approximately, all of which appear finely, though frequently sparsely, pilose. The whole shield has numbers of pores and the posterior half bears about a dozen or so pairs of very fine short setae (*c.* 20μ).

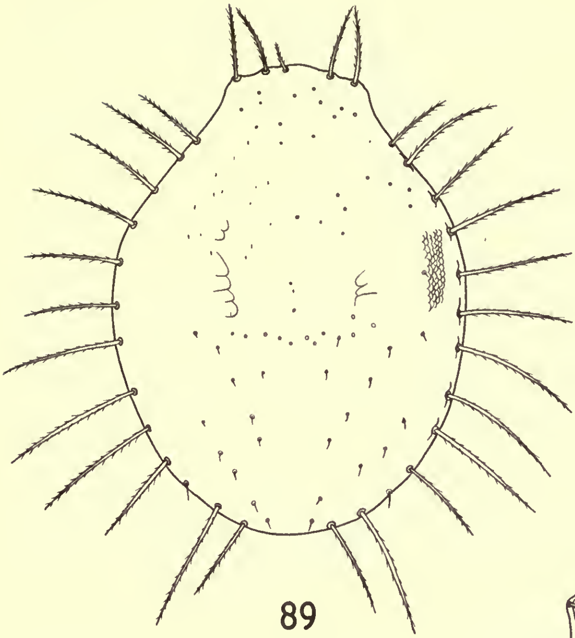
Tritosternum with a narrow base and pilose laciniae. Sternal shield approximately square with slightly concave lateral and anterior margins ; posterior projections extending to the metasternal setae, and posterior margin strongly concave (Text-fig. 90). The three pairs of sternal setae usually with fine pectinations. Metasternal setae similar to sternal setae but may lack pectinations. Latigynial and mesogynial shields fused with the ventral shield (Text-fig. 91). The ventral shield bears four pairs of setae, decreasing progressively in length posteriorly. Anal shield with two pairs of simple setae and several pores. The large metapodal shields, which extend posteriorly almost abutting the anal shield, bear two fine pairs of setae posteriorly. The stigma is situated between coxae III and IV and the peritreme extends to the anterior margin of coxa I. All ventral shields strongly sclerotized and striated.

Venter of gnathosoma as shown in Text-figure 92. The corniculi resemble slender blades with the inner margins serrated. The rostral setae are the stoutest and quite plain, although the posterior rostrals and the shorter capitulars may be lightly pilose. Palptarsal setae simple : remaining palpal setae with some fine pilosity. Apotele slender, two pronged. Fixed digit of chelicera with about 15 irregularly-shaped teeth ; movable digit with also about 15 subequal teeth and one large basal tooth. Fixed digit with a fringed membrane in its basal half ; movable digit with two large laciniate excrescences directed anteriorly, and the more distal one following the curve of the digit. The synarthrodial membrane at the base of the movable digit is cone shaped (Text-fig. 93). Tectum triangular with curved sides (Text-fig. 94).

Leg I about 880μ long, without ambulacrum ; some setae with fine pectinations. Legs II–IV stout, each with a pulvillus and two claws ; setae mainly stouter than on leg I, and some with fine pectinations.

MALE : Dorsal shield (920–1,000μ long × 705–760μ wide) similar in structure and chaetotaxy to the female.

FIGS. 89–96. *Euzercon balzani* Berlese. Fig. 89 dorsal shield of female. Fig. 90 venter of female. Fig. 91 intercoxal region of female. Fig. 92 venter of gnathosoma of female. Fig. 93 chelicera of female. Fig. 94 tectum of female. Fig. 95 intercoxal region of male. Fig. 96 venter of gnathosoma of male.



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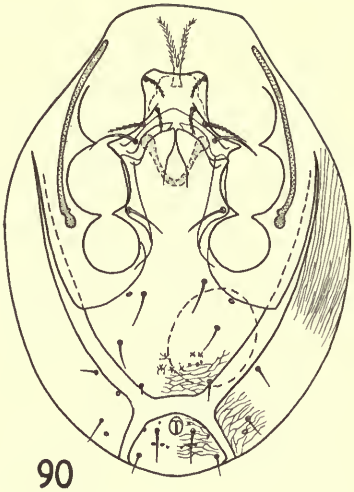

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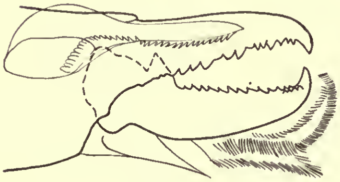

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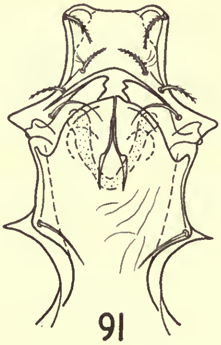

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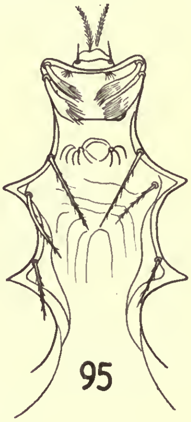

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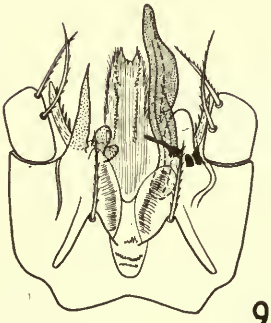

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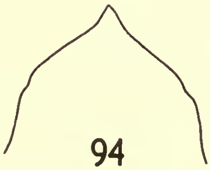

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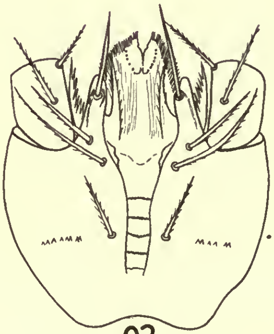

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The sterniti-genital region (Text-fig. 95) bears five pairs of setae : the two anterior pairs being stout and brush like, the remaining three pairs being slender and finely pilose. The remaining sclerotization and chaetotaxy of the venter is similar to the female.

Venter of gnathosoma shown in detail in Text-figure 96. Corniculi with inner margins serrated as in the female. Chaetotaxy of pedipalps similar to the female. The tectum and chelicerae also are very similar to the female.

Leg I 750µ long, without ambulacrum : some setae with fine pectinations. Legs II–IV stout, similar to the female.

Distribution : Berlese (1888) based his description of *E. balzani* on specimens taken under rotting leaves at Río Apa, Paraguay, and Lombardini (1940) redescribed and figured the species. Turk (1948), in recording *balzani* from a passalid beetle at Piarco, Trinidad, establishes the first record of this species from a beetle host. The present collection contains many males and females from the following beetles : *Passalus ? flascala* Perch (Col., Passalidae) (1387), Pie del Cerro, January 1956 ; Passalidae (2257 and 2258), Copey, September 1956 ; Passalidae (2329), Mérida, 3 December 1956 ; Passalidae (2639, 2640, 2651, 2675 and 2676), Río Caura, Bolívar, May 1957 ; *Passalus ? flascala* (2872, 2932 and 2933), Cabure, 12–14 December 1957 ; Passalidae (3256), San Juan de Manapiare, Amazonas, April 1958.

Family Klinckowstroemiidae

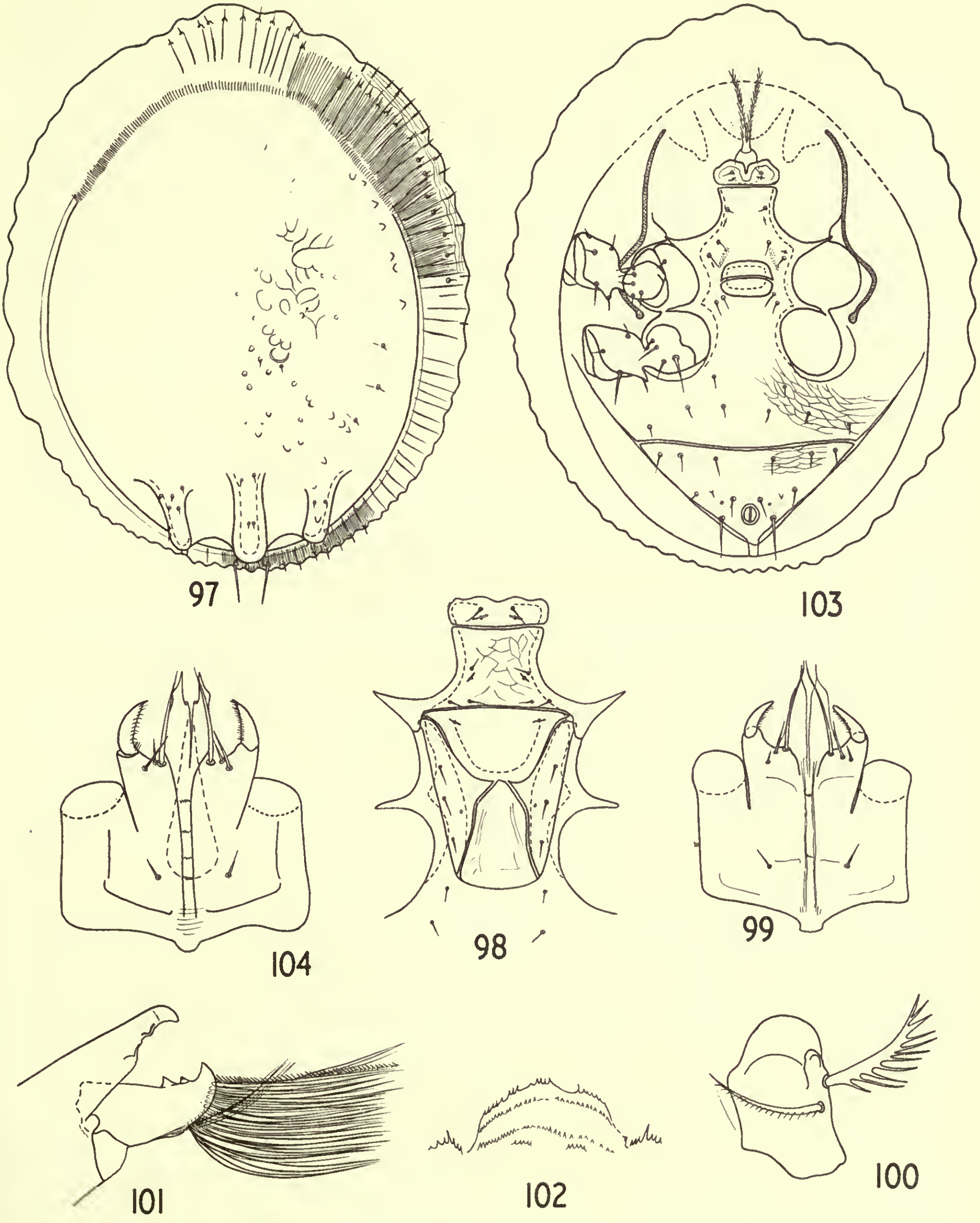
Genus *ANTENNURELLA* Berlese

Antennurella trouessarti Berlese, 1904

Antennurella trauessarti Berlese, A. 1904. Redia **1** : 268.
Antennurella trauessarti Lombardini, G. 1940. Bull. Soc. ent. Ital. **72** : 10, redescription, figs.

Female : Dorsal shield (1,080–1,140µ long × 930µ wide) encircled completely by a translucent hood-like extension of the shield which is up to *c.* 125µ broad anteriorly, decreasing to *c.* 15µ broad posteriorly (Text-fig. 97). The ornamentation of the shield comprises rather irregularly-scattered small tubercles, and posteriorly, three backward-projecting finger-like tubercles which extend slightly beyond the margin of the dorsal shield. The chaetotaxy of the dorsal shield comprises barely-discernible minute setae arising from some of the small tubercles, while the hood-like extension to the shield bears a number of short fine setae situated radially, and one pair of stouter setae, *c.* 75µ long, postero-medially.

Tritosternum with a pentagonal base and two pilose laciniae. Jugular shields coalesced with each other, and each bearing a simple slender seta. Sternal shield as broad as long, very finely reticulated, and bearing three pairs of simple setae ; one pair being central and the other two pairs on the posterior margin of the shield (Text-fig. 98). Posterior margin of sternal shield slightly concave ; the sternogynial shield hinged to this margin. Latigynial shields each with three simple setae ; mesogynial shield three-quarters as broad as long, faintly reticulated. Ventral shield posterior to coxae IV with four pairs of simple setae. Ventrianal shield with five pairs of simple slender preanal setae, paranal setae stouter and longer,



FIGS. 97–104. *Antennurella trouessarti* Berlese. Fig. 97 dorsal shield of female. Fig. 98 intercoxal region of female. Fig. 99 venter of gnathosoma of female. Fig. 100 right palptrochanter of female, ventrally. Fig. 101 chelicera of female. Fig. 102 tectum of female. Fig. 103 venter of male. Fig. 104 venter of gnathosoma of male.

postanal seta absent (see Text-fig. 103 of male). Stigma situated between coxae III and IV, peritreme finely granular and extending anteriorly to coxae I. Ventral shields heavily sclerotized and with fine reticulations. Endopodal and exopodal shields fused with the ventral shields.

Venter of gnathosoma shown in Text-figure 99. Corniculi with a fringe on their inner margins. Rostral setae long and stout, internal posterior rostrals longer than external posterior rostrals. Chaetotaxy of pedipalp simple except for the trochanter which bears two unusually-developed setae on its inner ventral margin : one being antler-like with about ten tines, the other pilose along one margin (Text-fig. 100). Apotele two pronged and slender. Fixed digit of chelicera with three teeth, less well developed in some specimens ; movable digit with two prominent teeth and a broad erect brush-like appendage, one-and-a-half times the length of the digit (Text-fig. 101). Tectum very difficult to discern, but comprising several transverse recurved rows of fine denticles, the lateral ones being the more prominent (Text-fig. 102).

Leg I with simple setae more dense on the tip of the tarsus ; without ambulacrum. Legs II–IV stout ; each with a well developed pulvillus and two claws. Femora each with an internal spur (as illustrated for the male, Text-fig. 103). Numbers of the setae with faint pilosity. Tarsi II–IV each have an erect straight dorsal seta distally.

MALE : Dorsal shield (1,090–1,190µ long × 850–950µ wide) very similar in structure and ornamentation to the female.

The venter is shown in detail in Text-figure 103. Tritosternum as in the female. Jugularia coalesced with each other but with a median suture ; each bearing a single seta. Sterniti-geniti-ventral region entire ; intercoxal region bearing six pairs of short simple setae. Region posterior to coxae IV with four pairs of simple setae. Genital aperture, located between coxae III, oblong-oval in shape, wider than long, and closed by two shields. Ventrianal shield as in the female : five pairs of short slender preanal setae, a pair of longer paranal setae, postanal seta absent. Stigma between coxae III and IV ; peritreme extending forward to coxa I.

Venter of gnathosoma shown in Text-figure 104 : similar to that of the female, apart from one factor which is constant in the four females and five males in the present collection : that is in the female the internal posterior rostral seta is longer than the external posterior rostral, but in the male the external posterior rostral is longer than the internal. Chaetotaxy and apotele of the pedipalp as in the female. Chelicerae as in the female. Tectum similar to the female.

Chaetotaxy of the legs as in the female.

DISTRIBUTION : Berlese (1904) described this species from a single male on *Passalus* sp. at Parà, Brazil. The present collection contains three males and two females from a passalid beetle (3256), San Juan de Manapiare, Amazonas, April 1958 ; one male from *Passalus ? flascala* Perch (Col., Passalidae) (2257), Copey, September 1956 ; one male from a passalid (2675), Río Caura, Bolívar, May 1957 ; and one male and one female from *Passalus ? flascala* (2872) at Cabure, 12 December 1957.

Genus *KLINCKOWSTROEMIELLA* Turk

Klinckowstroemiella prima Turk, 1951

Klinckowstroemia sp. (sp. n. ?) Turk, F. A. 1948. Proc. zool. Soc. Lond. **118** : 96.
Klinckowstroemiella prima Turk, F. A. 1951. Ann. Mag. nat. Hist. (12). **4** : 409.

FEMALE : Dorsal shield (764–848μ long × 550–600μ wide) smooth with areas of very fine reticulation and bearing some extremely fine short setules arising from pores. Anteriorly a hood-like extension of the dorsal shield (which is characteristic of the family) bears two pairs of fine setae each arising from a smooth tubercle (Text-fig. 105).

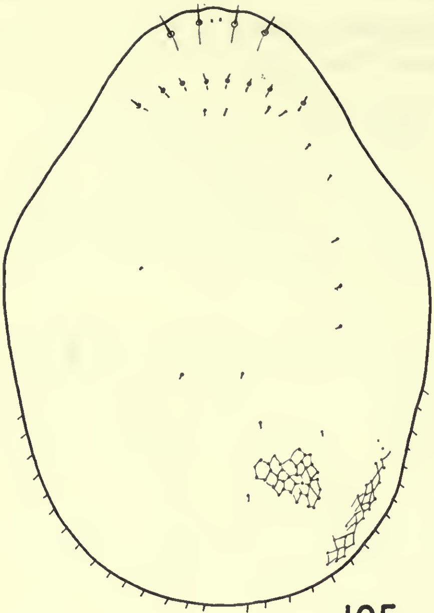
Tritosternum with a broad triangular base mainly concealed by the fused jugular shields. Laciniae strong with fine pilosity (Text-fig. 106). The single jugular plate bears one pair of short setae. Sternal shield trapezium shaped, fused with the endopodal plates, and bearing three pairs of simple setae. Sternogynial shield bearing one pair of pores and hinged to the posterior margin of the sternal shield. Latigynial shields with usually four pairs of short setae (as figured), but in a few specimens the setae are not paired, and odd combinations occur with six being the maximum. In these cases all sternal setae are longer than in the typical form. Mesogynial shield dome shaped. Ventral shield posterior to the genital area entire, finely reticulated, and bearing, in the figured specimen, 56 unpaired setae, of which the paranals are the longest. Stigma situated between coxae III and IV ; peritreme finely granular, extending to the anterior region of coxa II. Lateral to the stigma are five to seven denticles. Fused peritrematal-metapodal shield abutting the ventral shield.

Venter of gnathosoma shown in Text-figure 107. Corniculi bifid anteriorly. Rostral setae long and slender ; internal posterior rostrals longer than external posterior rostrals ; capitular setae short. Chaetotaxy of pedipalp simple except for the trochanter which bears two strongly-developed setae on its inner margin: one being antler like with about ten tines, the other pilose along one margin (Text-fig. 108). Apotele two pronged. Fixed digit of the chelicera with two large and four small teeth. Movable digit with two large teeth only, and with a broad erect brush-like process one and a half times the length of the digit (Text-fig. 109). The tectum, which is very difficult to discern, is shown in Text-figure 110.

Leg I slender ; with slender setae, and without ambulacrum. Legs II–IV stouter, with ambulacra ; femora each with a broad crassate ridge which is more pronounced in femora III and IV (Text-fig. 111).

MALE : Dorsal shield (733–795μ long × 507–550μ wide) similar in structure and chaetotaxy to the female.

Except for the intercoxal region, which is shown in detail in Text-figure 112, the ventral sclerotization and chaetotaxy are as in the female. The almost circular genital aperture, which is situated between coxae III, is covered by two shields divided laterally. The sternal shield anterior to the genital aperture bears three pairs of simple setae, whilst posterior to the aperture, very minute spicules only are present. The entire sternal shields are finely reticulated.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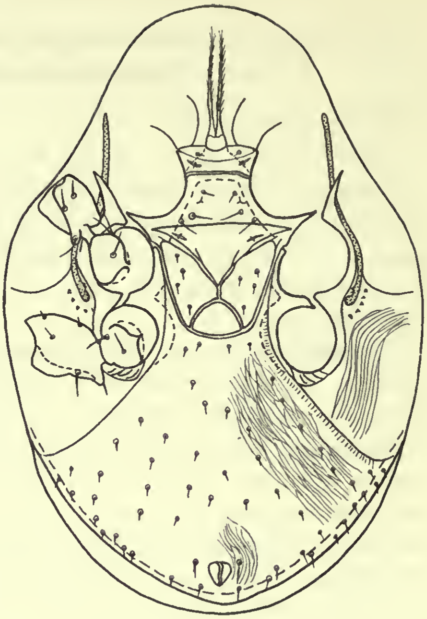
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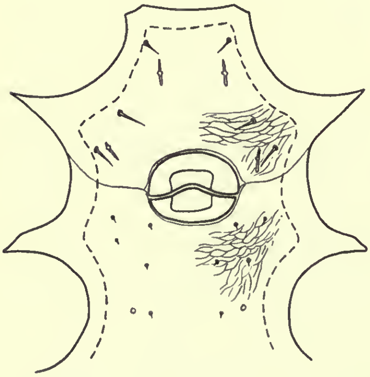
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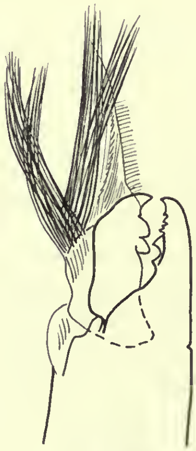
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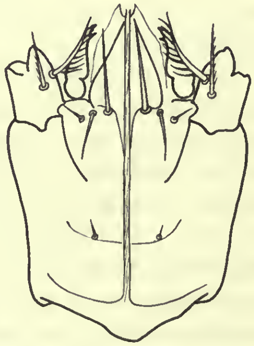
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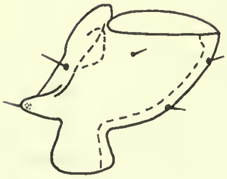
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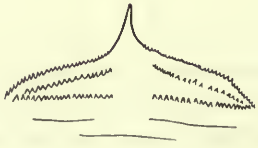
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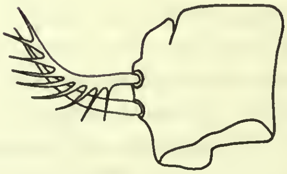
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Venter of gnathosoma basically the same as in the female, although generally the internal posterior rostrals are longer than in the female. Chaetotaxy of the pedipalp as in the female. Chelicerae and tectum also as in the female.

Chaetotaxy of all legs, and protuberances on femora II–IV as in the female.

DISTRIBUTION : Turk's (1948) specimens are from a passalid beetle collected at Trinidad, British West Indies. The present collection contains 16 males and 54 females on passalids (2612, 2639, 2640 and 2676), Río Caura, Bolívar, May 1957 ; and one male and four females on a passalid (3256), San Juan de Manapiare, Amazonas, April 1958.

The above description is based entirely on the specimens from Venezuela. I have, through the kindness of Dr. F. A. Turk, examined the types of *K. prima*, and although the size of his specimens (one male 962μ long × 722μ wide, and four females 953–983μ long × 711–743μ wide) far exceeds the range of the Venezuelan material, there are no clear differences in the structure or chaetotaxy of the dorsum. venter, gnathosoma, or legs.

FAMILY PARAMEGISTIDAE

Genus ***ECHINOMEGISTUS*** Berlese

Echinomegistus narvaezi sp. nov.

FEMALE : Dorsal shield (930–952μ long × 805–826μ wide) heavily sclerotized and subcircular in outline (Text-fig. 113). Two simple setae situated vertically are probably the only setae actually located on the dorsal shield, although a small number of extremely minute setules may arise from some of the numerous pores and minute warts which are spread over the entire shield. On the interscutal membrane between the dorsum and venter of the mite is a narrow continuous strip of cuticle extending posteriorly from the region of coxae III, and bearing in the region of 96 stout setae, of which every second or third seta is longer than the intermediate ones.

The tritosternum has a narrow conical base and pilose laciniae. Jugular shields trapezium shaped and bearing a single pair each of setae and pores ; the setae being noticeably stouter than the other sternal setae (Text-fig. 114). In some specimens the inner corners of the jugularia are rounded, therefore the shields are further apart. Sternal setae II, III and IV are situated on the endopodal shields ; the latter extending till they meet medially. Sternogynial shield divided medially. Latigynial shields, bearing two pairs of simple setae, hinged to the ventral shield to a variable degree : in some specimens there is almost no trace of a division between the latigynial and sternal shields. Mesogynial shield in the form of an isosceles triangle. Ventral shield posterior to the genital area flask shaped and bearing between 25 and 30 pairs of strong lanceolate setae *c.* 75μ in length (Text-fig. 115). Posterior to the anus, and on the border of the ventral shield, are from four to five

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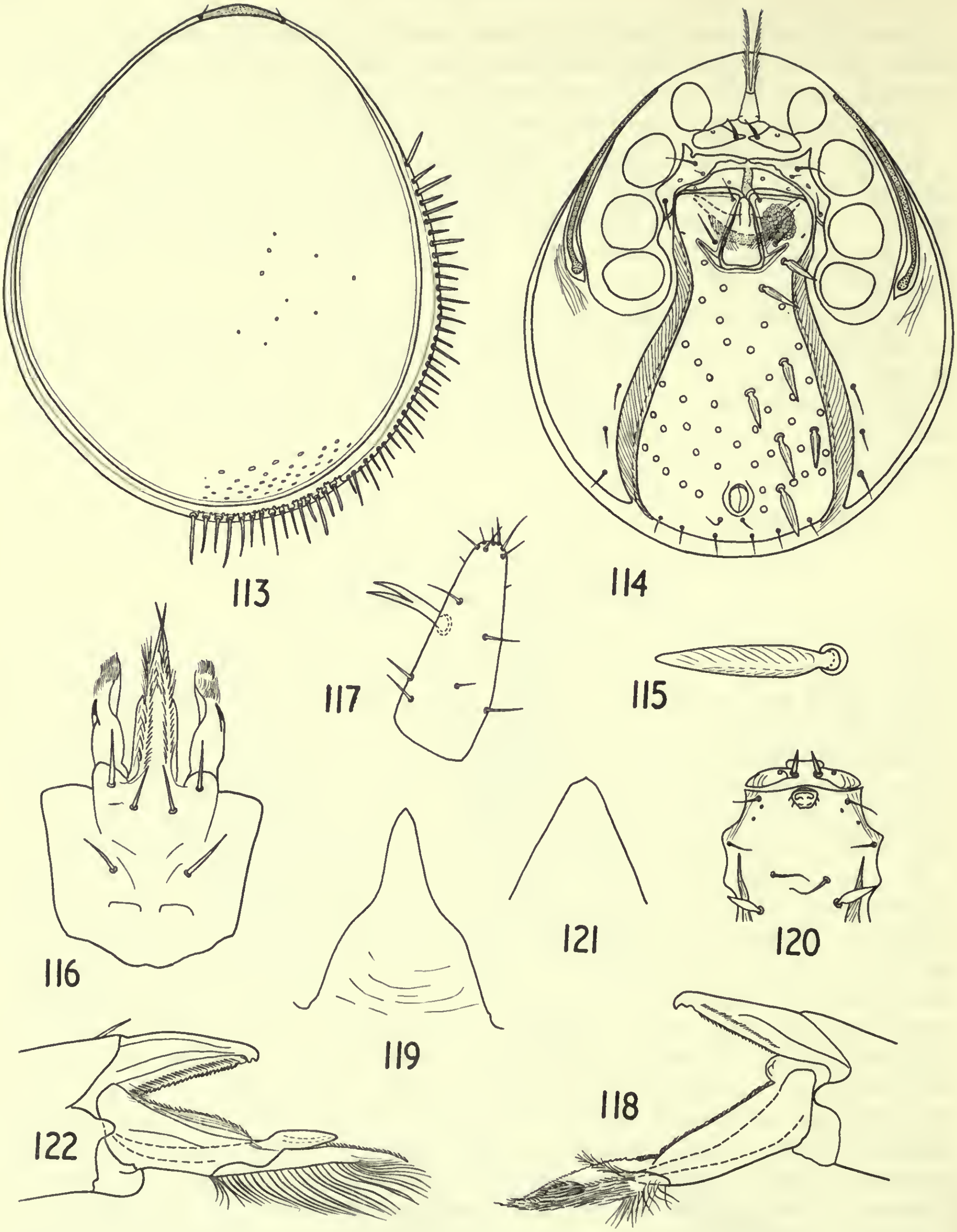
FIGS. 105–112. *Klinckowstroemiella prima* Turk. Fig. 105 dorsum of female. Fig. 106 venter of female. Fig. 107 venter of gnathosoma of female. Fig. 108 palptrochanter of female. Fig. 109 chelicera of female. Fig. 110 tectum of female. Fig. 111 right femur IV of female, ventrally. Fig. 112 intercoxal region of male.



FIGS. 113–122. *Echinomegistus narvaezi* sp. nov. Fig. 113 dorsum of female. Fig. 114 venter of female. Fig. 115 ventral seta of female. Fig. 116 venter of gnathosoma of female. Fig. 117 fused palp tarsus and tibia of female, ventrally. Fig. 118 chelicera of female. Fig. 119 tectum of female. Fig. 120 genital region of male. Fig. 121 tectum of male. Fig. 122 chelicera of male.

pairs of fine simple setae. The stigma is situated opposite coxa IV and the peritreme extends in a smooth curve to the centre of coxa I. The broad posterior prolongation of the metapodal shields tapers to terminate level with the posterior margin of the anus. The inner margin of the metapodal shield bears three or four simple slender setae.

Venter of gnathosoma shown in Text-figure 116. Corniculi membranous with a finger-like process midway. Rostral setae modified into long slender laciniate processes ; posterior rostral and capitular setae simple and of equal length. Palp tarsus and tibia fused, and with two-pronged apotele situated midway on the segment (Text-fig. 117) ; chaetotaxy of pedipalp simple. Fixed digit of chelicera slender, with two rows of fine saw-like teeth ; one row anteriorly, the other posteriorly, directed (Text-fig. 118). Movable digit with two excrescences, one long and membranous with a finely-serrated margin, the other brush-like and filamentous ; digit with saw-like teeth similar to the fixed digit. Tectum regular in outline, conical-triangular with a construction midway (Text-fig. 119).

Leg I (*c.* 1,030µ long) without ambulacrum, slender ; chaetotaxy simple. Legs II–IV stouter ; chaetotaxy comprising shorter setae than leg I, a few setae, however, pilose distally.

Male : Dorsal shield (826–900µ long × 682–795µ wide) essentially the same as in the female. Stout interscutal setae equal in number and form to the female.

The genital region is shown in detail in Text-figure 120. Jugularia somewhat similar to those of the female ; the setae on these shields being stouter than the remaining sternal setae. Genital aperture small, situated between coxae II. Three pairs only of simple setae in the genital region. Ventral shield posterior to the genital area flask-shaped as in the female, but bearing only 21–24 pairs of strong lanceolate setae. Posterior to the anus, and on the border of the ventral shield, are four pairs of fine simple setae. Stigmata, peritremes and metapodal shields as in the female, and with also three pairs of simple setae on the inner margin of the metapodal shield.

Venter of gnathosoma essentially the same as in the female. Pedipalp as in the female. The tectum and chelicera are shown in Text-figs. 121 and 122 respectively.

Leg I without ambulacrum ; legs II–IV with a pulvillus and two claws. Chaetotaxy of legs similar to the female.

Localities : The holotype female (1963.10.3.238) and allotype male (1963.10.3.237) and 53 paratypes of both sexes (1963.10.3.239–248) from *Encaladus gigas* Bonelli (Col., Carabidae) (2236), Cerro Atagua, Margarita, Venezuela, 27 August 1956 ; and one paratype male (1963.10.3.249) from *Passalus flascala* Perch (Col., Passalidae) (2256), Margarita, September 1956.

Echinomegistus narvaezi is obviously related to *E. wheeleri* (Wasm.) which is figured by Berlese (1904) and also by Trägårdh (1943). The latter author, who examined specimens from Copenhagen Museum, commented favourably on Berlese's drawing of the venter of *wheeleri*. The present species differs from *wheeleri* in possessing far less setae ventrally, both on the geniti-ventral shield and the metapodal shields, and also on the interscutal cuticle around the posterior half of the mite. *E. wheeleri* is also a larger species.

Echinomegistus narvaezi is dedicated to Senor Heraclio Narváez Lafonzo, Governor of Isla Margarita.

SUMMARY

Twenty-six species of mesostigmatid mites associated with Venezuelan Coleoptera and Hemiptera are described and figured. The following sixteen species are considered new to science :

Zygoseius tectus sp. nov.
Gaeolaelaps circularis sp. nov.
Hypoaspis passali sp. nov.
Coleolaelaps metasternalis sp. nov.
Coleolaelaps coxalis sp. nov.
Coleolaelaps striatus sp. nov.
" *Coleolaelaps* " *granulatus* sp. nov.
" *Coleolaelaps* " *latisternalis* sp. nov.
Brachytremella womersleyi sp. nov.
Trichodiplogynium carlosi sp. nov.
Heterodiplogynium secundum sp. nov.
Brachysternum espinozai sp. nov.
Brachysternum cornutum sp. nov.
Tridiplogynium brenthi sp. nov.
Cryptometasternum diazungriai sp. nov.
Echinomegistus narvaezi sp. nov.

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STEATONYSSUS KOLENATI
(ACARI: MESOSTIGMATA)

W. M. TILL & G. OWEN EVANS

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ZOOLOGY Vol. 11 No. 8
LONDON: 1964

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W. M. TILL & G. OWEN EVANS
British Museum (Natural History)

Pp. 511–582 ; 82 *Text-figures*

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STEATONYSSUS KOLENATI
(ACARI: MESOSTIGMATA)*

By W. M. TILL & G. OWEN EVANS

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SYNOPSIS

The external morphology and classification of the macronyssine genus *Steatonyssus* Kolenati are reviewed. Twenty-six species and subspecies are recognized, five of which are considered new. A further seven species are treated as *species incertae sedis.* A key is given for the identification of females.

INTRODUCTION

THE present review of the genus *Steatonyssus* Kolenati is the second in a series of revisionary studies on the Macronyssinae (family Laelaptidae). The first, dealing with the genus *Pellonyssus* Clark and Yunker, was undertaken by Till (1964). Members of both genera differ from other macronyssines in having two distinct dorsal shields (the podonotal and opisthonotal) in the female. Species of *Steatonyssus* are, with few exceptions, ectoparasites of bats (Chiroptera) whereas those of *Pellonyssus* occur only on birds.

This study is based on material in the collections of the British Museum (Natural History) and on specimens kindly sent to us by Dr. V. Aellen, Muséum d'Histoire Naturelle, Geneva ; Dr. P. L. G. Benoit, Musée royal de l'Afrique centrale, Brussels ; Dr. F. Radovsky, George Williams Hooper Foundation, San Francisco and by Dr. F. Zumpt, South African Institute for Medical Research, Johannesburg. We have also examined type material from the Kolenati and Oudemans Collections by the kind permission of Dr. M. André, Paris, and Dr. L. van der Hammen, Leiden, respectively. Dr. N. Bregetova, Zoological Institute of the Academy of Sciences, Leningrad, kindly arranged for the loan of *Steatonyssus primus* Grokhovskaya et al. and *S. secundus* Grokhovskaya et al., and Dr. E. W. Baker, United States National Museum, allowed us to borrow types of Ewing's and Delfinado's species.

EXTERNAL MORPHOLOGY

The following account of the external morphology of the genus *Steatonyssus* refers to the active feeding stages only, the protonymph, female and male. We have not examined larvae or deutonymphs.

GNATHOSOMA :

The cheliceral shafts in the protonymph and female are relatively stouter than in members of the genus *Pellonyssus*, the second segment being two and one-half to six times as long as the first segment. The digits are slender, edentate and about 25–50μ in length (Text-fig. 3). In the males the second cheliceral segment is two to four times the length of the first. Both digits are essentially edentate in the male. The fixed digit is slender and has a rounded tip with an expanded hyaline margin. The movable digit, which has an overall length of at least two-thirds that of the second segment, consists of three parts, a dorsal process about as long as the fixed digit, a longer, grooved, ventral spermadactyl, and an intermediate hyaline process (Text-fig. 2).

The gnathosomal setae show a parasitoid arrangement. There are no well-defined corniculi and the deutosternal denticles are arranged in a single file (Text-fig. 1). The transparent, tongue-shaped tectum has a fimbriated apex (Text-fig. 4).

The pedipalp has five free segments and a two-tined apotele. In the female of all the known species except *Steatonyssus furmani* Tipton and Boese, a large process is developed on the antero-ventral surface of the palptrochanter. This process is not present in the males or in the protonymphs. The chaetotaxy of the pedipalp is shown in Text-fig. 6–7 and the chaetotactic formulae are as follows :—

Protonymph (1 – 4 – 5 – 12 – 15)
Adult (2 – 5 – 6 – 13 – 15)

The protonymphal pedipalpal chaetotaxy is normal but the chaetotaxy of the palptibia in the adult is unideficient, fourteen setae being normally present on this segment in the free-living Laelaptidae (Evans, 1964).

IDIOSOMA :

Dorsum. The dorsal sclerotization of the protonymph consists of a podonotal shield, two to four pairs of mesonotal scutellae and a pygidial shield (Text-fig. 48, 66). In the female the mesonotal and pygidial shields fuse to form the opisthonotal shield. In the males, except *S. furmani* which retains the female condition, all the dorsal shields fuse to form a single scutum which may be far more expanded than in the female.

In the few species examined (*S. antrozoi*, *S. calcaratus*, *S. javensis* s. lat., *S. longipes*, *S. periblepharus* and *S. tibialis*) the podonotal shield of the protonymph bears 11 pairs of setae, *i2* being present (Text-fig. 43). Unfortunately we have not been able to examine the protonymphs of any of the species which lack seta *i2* in the adult stage. On the posterior part of the dorsum setae *J1* – *J3* are situated on the striated integument. The pygidial shield usually bears three pairs of relatively long, stout setae (*Z4*, *Z5* and *S5*) and one pair of minute subterminal setae (*J5*). The subterminals are lacking in *S. antrozoi* and *S. calcaratus*, and also in *S. furmani* (Radovsky and Furman, 1963). Setae *J4* are absent throughout the genus. In the majority of species the female also bears 11 pairs of setae on the podonotal shield and seven pairs on the opisthonotal shield. However, setae *i2* may be lacking, as in *S. evansi*, *S. benoiti* and *S. sudanensis*, or additional marginal setae may be incorporated, thus increasing the number on the podonotal shield to 16 pairs as in *S. furmani*. The opisthonotal shield may lack the subterminal setae, as in *S. antrozoi*, *S. calcaratus*, *S. evansi* and *S. furmani*, or both the terminal and subterminal setae may be absent as in *S. benoiti* and *S. sudanensis*. Varying degrees of hypertrichy are also encountered, for example, in *S. eos*, *S. brucei*, *S. crassisetosus* and *S. nyassae*. In the male the chaetotaxy of the dorsal shield is usually the same as that of the combined anterior and posterior shields in the female, except that additional marginal setae are sometimes incorporated. In *S. brucei* and *S. crassisetosus* this process has gone further than in any of the other known species, the number of setae on the scutum exceeding 30 pairs.

Venter. The tritosternum in all stages resembles that of *Pellonyssus*, consisting of a narrow basal portion and a pair of laciniae. A hyaline denticulate membrane extends along the external margin of the base and continues as a narrow border along the laciniae.

The sternito-genital region in the protonymphs bears three pairs of sternal setae and one pair of genitals at the level of coxae IV (Text-fig. 67). A pair of metasternal setae (normally developed at the deutonymphal stage in the Gamasina) is present in the adults. In the female the posterior part of the sternal shield is differentiated to a varying degree from the anterior part, except in *S. furmani* in which there is no apparent distinction. The differentiation may be very slight and indicated only by the more narrowly spaced reticulations in the posterior area, as in *S. hipposideros* and in *S. javensis* s. lat. In most species, however, the posterior portion is heavily sclerotized and may form a dense band. The anterior part of the shield usually has a reticulate pattern similar to that of the presternal area. The shield bears the usual two pairs of pores, but it is not possible to distinguish a third pair near the metasternal setae. The anal shield shows very little variation in the species examined. It is triangular in the protonymphs, pear-shaped in the females, and the par- and postanal setae are subequal in length. The paranal setae are level with the posterior half of the anus except in *S. benoiti* and *S. eos* in which they are situated posterior to the anus. The ventral armature is fused to form a holoventral shield in all the known males except *S. furmani* which has three separate shields, sternito-genital, ventral and anal. The number of setae in the preanal region is subject to intraspecific variation. The genital orifice is presternal.

The chaetotaxy of the unsclerotized surface of the idiosoma of the adults shows interspecific variation with respect to the relative lengths and the form of the posterior setae. The peritremes are short in the protonymphs and extremely variable in length in the adults. In *S. longipes* and *S. tibialis* for example, they terminate at a point level with the middle of coxa III, whereas in *S. javensis* they extend as far as the anterior fourth of coxa II. In the females of some species, for example *S. brucei*, *S. nyassae*, *S. periblepharus* and *S. spinosus*, the peritrematal shields continue anteriorly in the form of broad, leaf-like structures which lie on the dorsal surface of the body over coxae I and II (Text-figs. 45, 62). In most of the American and also in some of the African species (e.g. *S. afer*, *S. eos*, *S. hipposideros*, *S. longipes*, *S. natalensis*, *S. sudanensis*) this shield is interrupted in front of the peritremes (Text-figs. 24, 34). The males do not have this expanded leaf-like portion, the peritrematal shields terminating in a short point immediately anterior to the peritreme. In all the adults examined the peritremes are fused posteriorly with the podal elements of coxa IV. Small endopodal plates are usually present between coxae III and IV and indistinct metapodal plates may be visible behind coxae IV.

Legs. As in the genus *Pellonyssus*, all the legs are six-segmented, excluding the terminal ambulacrum comprising a pulvillus and two claws. The femora and tarsi of all the legs are incompletely divided by transverse fissures and a lyriform fissure is present on the distal half of tarsi II–IV. The second coxa bears a pronounced antero-dorsal spine in all the species examined. In the usual position of the coxae in mounted specimens, this spine has a simple, triangular appearance. However, if the spine is viewed from a lateral angle its tip often appears denticulate (Text-fig. 5a, b).

In the protonymphal stage the chaetotaxy of the legs is the same as in the genus *Pellonyssus* (Till, 1964). In the females examined the chaetotaxy differs from that of *Pellonyssus* in several respects. Legs I and II have the typical laelaptid pattern as defined by Evans (1963). Seta v_4 is present on femur I, whereas it is absent in all the *Pellonyssus* species except *P. reedi*. Tibia I bears seta pd_3 in all the *Steatonyssus* species examined, except *S. sudanensis*, but lacks this seta in all the *Pellonyssus* species. On femur III the ventral seta is always proximal to the fissure in *Steatonyssus*, but may be either proximal or distal in *Pellonyssus*. Tibia III has ten setae in *S. tibialis*, ad_2 being present $(2-\frac{2}{1}, \frac{2}{1}-2)$, but nine in all the other species examined, as in *Pellonyssus*. Free-living laelaptids have only eight setae on tibia III. Genu IV has only one postero-lateral seta, whereas all the *Pellonyssus* species have two. Tibia IV has 11 setae in *S. tibialis*, ad_2 being present $(2-\frac{2}{1}, \frac{3}{1}-2)$, whereas in all the other species examined there are only ten setae, as in *Pellonyssus* and the free-living Laelaptidae. The typical chaetotactic formulae for the femora, genua and tibiae of the legs of the adults may be expressed as follows :—

	I	II	III	IV
Femur	$2-\frac{5}{4}-2$	$2-\frac{5}{3}-1$	$1-\frac{3}{1}-1$	$1-\frac{3}{1}-1$
Genu	$2-\frac{3}{2}, \frac{3}{1}-2$	$2-\frac{3}{1}, \frac{2}{1}-2$	$2-\frac{2}{1}, \frac{2}{1}-2$	$2-\frac{2}{1}, \frac{3}{1}-1$
Tibia	$2-\frac{3}{2}, \frac{3}{1}-2$	$2-\frac{2}{1}, \frac{2}{1}-2$	$2-\frac{1}{1}, \frac{2}{1}-2$	$2-\frac{1}{1}, \frac{3}{1}-2$

CLASSIFICATION

There is considerable confusion in the literature concerning the status of certain species which have been assigned to the genus *Steatonyssus*. When Kolenati (1858) erected the genus he included in it only two species, *S. periblepharus* Kol. and *S. brachypeltis* Kol. The latter is now considered a junior subjective synonym of the former which becomes the type of the genus. In 1922 Hirst proposed the taxon *Liponyssus chiropteralis* for a species having two dorsal shields and living on bats in Europe and North Africa because he was unable to relate the species with certainty to *S. periblepharus*, *Liponyssus musculi* (Koch) Oudemans or *Dermanyssus arcuatus* Koch. Oudemans (1936) considered both Kolenati's and Hirst's species, as well as *Dermanyssus murinus* Lucas, 1840 and *D. avium* Wagner, 1841, to be synonyms of *Dermanyssus vespertilionis* Dugès, 1834.

We have examined the type material of *L. chiropteralis* and *S. periblepharus* and are able to confirm that they are conspecific. The type material of *D. murinus*, *avium* and *vespertilionis* must be presumed to be lost and their original descriptions are such as to make their specific identity impossible. The continued use of these names can only lead to further confusion and we, therefore, regard them as *species incertae sedis*.

Acarus musculi Schrank, 1803, a mite found on the skin of a house mouse, is the oldest described species assigned to the genus *Steatonyssus*. The original description, quoted by Oudemans (1936), is based on the shape and colour of the mite and is certainly not adequate for the certain identity of the species. The type material is not available but as there are no confirmed records of a *Steatonyssus* from mice, it seems unlikely that Schrank's mite can belong to this genus. Oudemans

(1936) lists *Dermanyssus musculi* Koch, 1836, also from house mice, as a synonym of *A. musculi*. The mite described by Oudemans (1902a) as *Liponyssus musculi* (Koch) is undoubtedly a *Steatonyssus* but it was collected from a bat and not a mouse, whereas the " deutonymph " of *L. musculi* described by him in 1903 (also from a bat) certainly does not represent a *Steatonyssus*—it is probably a protonymph of *Macronyssus*. In later papers (1912, 1913a & b) Oudemans lists bats and mice as hosts of *L. musculi* (Koch). It is obvious that *Liponyssus musculi* sensu Oudemans represents more than one species and the confusion has probably arisen because some of the records were based on immature stages which could not be identified with certainty at that time.

By courtesy of Dr. van der Hammen we have examined slide No. 2355 from the Oudemans Collection which is labelled " *Steato* (*Cerato-*) *nyssus musculi* Koch, from *Mus musculus albus*, Hamburg, July, 1921. The specimens represent six females of *Ornithonyssus bacoti* (Hirst)! This suggests that *A. musculi* Schrank and *D. musculi* Koch might possibly be conspecific with *O. bacoti*.

Strandtmann and Wharton (1958) consider *Liponyssus pipistrelli* Oudemans, 1904 to be a synonym of *Steatonyssus musculi* (Schrank). The specimen labelled *Liponyssus pipistrelli* from *Plecotus auritus*, Bodegraven, VIII, 1892, in the Oudemans Collection is a protonymph of *Macronyssus*. We cannot be sure, however, that this is the type specimen (see Buitendijk, 1945).

Liponyssus cyclaspis Oudemans (1906 a & b), which is known only from the protonymph, is also a species of *Macronyssus*. This is indicated in the drawing of the dorsum of the mite by Oudemans (1915) and has been confirmed by the examination of the type.

The systematic position of *Steatonyssus biscutatus* (Hirst) and consequently of the closely related *Pellonyssus trachyphoni* Till is somewhat problematical, as these species have some characters in common with *Steatonyssus* and others which are typical of *Pellonyssus* (Till, 1964). The features which they share with all *Steatonyssus* are the relatively large sternal shield in the female, the presence of metasternal setae and the position of the ventral seta on femur III. In common with all *Pellonyssus* they lack seta *i2* on the podontal shield and seta pd_3 on tibia I, and have two postero-lateral setae on genu IV. The chelicerae of the male of *P. trachyphoni* have the typical *Pellonyssus* and not the *Steatonyssus* structure. However, neither genus is completely homogeneous. Three of the *Steatonyssus* species, for example, lack seta *i2*, and *Pellonyssus similis* (Zumpt and Till) has a proximally situated ventral seta on femur III. The process on the palptrochanter is also a variable feature. It is present in half the known species of *Pellonyssus* and in all except one of the species of *Steatonyssus*. In fact the only reliable " key character " which can be used to separate the two genera is the chaetotaxy of genu IV, *Pellonyssus* having two postero-lateral setae on this segment and *Steatonyssus* only one. Clark and Yunker (1956) included *S. biscutatus* in their new genus *Pellonyssus* but Radovsky and Yunker (1963) restored it to the older combination. For the present we prefer to leave these two species in the genus *Pellonyssus*, with other bird-infesting forms.

Steatonyssus furmani Tipton & Boese displays a number of morphological features which immediately separate it from the other species which we have included in the genus *Steatonyssus*. In the female, the palptrochanter lacks an antero-lateral process and the podonotal shield carries sixteen pairs of setae. The male of *S. furmani* is unique in having two subequal dorsal shields (as in the female) and in having three distinct ventral shields (a sternito-genital, a ventral and an anal). On the basis of these morphological differences we propose a new subgenus *Steatonyssella* for the reception of *S. furmani* which becomes its type species.

DESCRIPTIONS OF SPECIES

Genus ***STEATONYSSUS*** Kolenati *s. lat.*

Steatonyssus Kolenati, F. A. 1858. *Wien. ent. Monatschr.*, **2** : 6 ; 1859 *S. B. Akad. Wiss. Wien*, **35** : 186.
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Ceratonyssus Ewing, H. E. 1923. *Proc. U.S. nat. Mus.*, **62** (2459) : 6.

TYPE : *Steatonyssus periblepharus* Kolenati, 1858.

KEY TO FEMALES OF THE GENUS *Steatonyssus* KOL. *s. lat.*

1 Palptrochanter with strong process (Text-fig. 7) ; podonotal shield with not more than 13 pairs of setae (subgenus *Steatonyssus*) 2
– Palptrochanter without process ; podonotal shield with 16 pairs of setae (subgenus *Steatonyssella*) . . . . ***S. furmani*** Tipton & Boese (p. 574)
2 Coxa III with pronounced spur bearing the posterior seta ***S. calcaratus*** Radovsky & Yunker (p. 531)
– Coxa III without such spur 3
3 Podonotal shield lacking seta *i2* (Text-fig. 28) 4
– Podonotal shield with seta *i2* (Text-fig. 62) 6
4 Opisthonotal shield with six pairs of setae (Text-fig. 28) . ***S. evansi*** Delfinado (p. 540)
– Opisthonotal shield with five pairs of setae (Text-figs. 8, 72) 5
5 Tibia I lacking seta pd_3 ; coxae II and III with spine-like posterior setae (Text-fig. 73) . . . . ***S. sudanensis*** (Hirst) (p. 569) .
– Tibia I with seta pd_3 ; coxae II and III with simple setae (Text-fig. 9) ***S. benoiti*** sp. nov. (p. 526)
6 Opisthonotal shield with setae *Z*5 about two and one-half times as long as the longest postero-marginal setae on the shield (Text-fig. 70) ***S. spinosus*** Willmann (p. 567)
– Opisthonotal shield with setae *Z*5 at the most only slightly longer than the longest postero-marginal setae 7
7 Tibia III with four dorsal setae ; tibia IV with five dorsal setae ***S. tibialis*** sp. nov. (p. 570)
– Tibia III with three dorsal setae ; tibia IV with four dorsal setae 8
8 Opisthonotal shield with six pairs of setae (subterminals absent) (Text-fig. 68) . 9
– Opisthonotal shield with seven or more pairs of setae (subterminals present) (Text-fig. 62) 10
9 Podonotal shield with 11 pairs of setae ; posterior margin of sternal shield with a strongly sclerotized band . . . . ***S. antrozoi*** Radovsky & Furman (p. 524)

– Podonotal shield with 13 pairs of setae (Text-fig. 68) ; posterior margin of sternal shield without a strongly sclerotized band . . . ***S. radovskyi*** sp. nov. (p. 566)

10 Opisthonotal shield with seven pairs of setae 11

– Opisthonotal shield with more than seven pairs of setae (unpaired setae often present) 21

11 Sternal setae I very short, not more than one-half the length of sternal setae II (Text-fig. 63) . . . . ***S. periblepharus*** Kolenati (p. 562)

— Sternal setae I at least two-thirds the length of sternal setae II (Text-fig. 17) . 12

12 Dorsal setae *i*2 minute, slender, at the most one-third the length of setae *i*3 (Text-figs. 16, 50) 13

– Dorsal setae *i*2 stronger, about one-half or more the length of setae *i*3 (Text-fig. 58) 15

13 Dorsal setae *i*3 about one-third the length of setae *z*1 (Text-fig. 16) ***S. ceratognathus*** (Ewing) (p. 532)

– Dorsal setae *i*3 almost two-thirds the length of setae *z*1 (Text-fig. 50) . . . 14

14 Dorsal setae *i*5 and *z*3 subequal in length ; opisthonotal shield tapering strongly in its proximal third . . . ***S. emarginatus*** Radovsky & Furman (p. 537)

– Setae *i*5 not more than two-thirds the length of *z*3 ; opisthonotal shield not tapering strongly in its proximal third (Text-fig. 50) . . ***S. joaquimi*** (Fonseca) (p. 553)

15 Sternal shield with a strongly sclerotized band posteriorly (Text-fig. 59) . . 16

– Sternal shield without such a sclerotized band, the shield having at the most, a more strongly defined area of ornamentation posteriorly (Text-figs. 40, 47) . 17

16 Setae *J*1–*J*3 relatively long ; length of seta *J*2 about equal to three-quarters the distance between the bases of *J*2 and *J*3 . ***S. afer*** Radovsky & Yunker (p. 521)

– Setae *J*1–*J*3 conspicuously shorter ; length of seta *J*2 about equal to one-third the distance between the bases of *J*2 and *J*3 (Text-fig. 58) ***S. occidentalis*** (Ewing) (p. 559)

17 Setae on the unsclerotized integument of the opisthonotum short (approx. 12–27μ in length) . . . . ***S. javensis*** (Oudemans) s. lat. (p. 547)

– Setae on the unsclerotized integument of the opisthonotum considerably longer and stronger (more than 50μ in length) 18

18 Peritreme reaching to the level of the anterior region of coxa II (Text-fig. 34) ***S. hipposideros*** Till (p. 544)

– Peritreme scarcely extending beyond the level of the posterior margin of coxa II . 19

19 Length of tarsus IV at least five times its basal width ; peritreme very short, reaching to about the middle of coxa III . ***S. longipes*** Radovsky & Yunker (p. 554)

– Length of tarsus IV less than four-and-one-half times its basal width ; peritreme longer, reaching up to or slightly beyond the level of the anterior margin of coxa III 20

20 Length of seta *J*2 about equal to one-third the distance between *J*2 and *J*3 ; antero-dorsal spur on coxa II with a broad, flattened serrated tip ***S. aelleni*** Radovsky & Yunker (p. 521)

– Length of seta *J*2 about equal to one-half the distance between *J*2 and *J*3 ; antero-dorsal spur on coxa II with a pointed tip lacking distinct serrations ***S. natalensis*** Zumpt & Patterson (p. 555)

21 Paranal setae some distance posterior to the anus. Posterior margin of the sternal shield not heavily sclerotized, anterior part of the peritrematal shield separate (Text-figs. 24, 25) . . . . ***S. eos*** Zumpt & Till (p. 538)

– Paranal setae never behind the posterior margin of anus. Posterior margin of sternal shield strongly sclerotized ; anterior part of the peritrematal shield continuous 22

22 Opisthonotal shield relatively broad, length not more than 1·2 times the width ; anterior process of the genital shield relatively short and broad (Text-figs. 30, 31) ***S. faini*** Delfinado (p. 542)

– Opisthonotal shield relatively slender, length at least 1·4 times the width ; anterior process of the genital shield relatively long, narrow, sharply pointed (Text-figs. 13, 21) 23

23 Setae *i2* of the podonotal shield long, extending up to or beyond the bases of setae *i3* (Text-fig. 56) . . . . **S. nyassae** (Hirst) (p. 558)

– Setae *i2* of the podonotal shield considerably shorter, reaching to about one-half the distance between the bases of setae *i2* and *i3* (Text-fig. 12). 24

24 Setae *S5* on the opisthonotal shield less than three-quarters the length of the terminals (*Z5*) ; posterior integumental setae stout, tapering gradually (Text-fig. 12) . . . . **S. brucei** Lavoipierre (p. 528)

– Setae *S5* on the opisthonotal shield longer than the terminals (*Z5*) ; posterior integumental setae rod-like, tapering only at the tips (Text-fig. 20) **S. crassisetosus** sp. nov. (p. 534)

Subgenus **STEATONYSSUS** *s. str.*

Steatonyssus (Steatonyssus) aelleni Radovsky & Yunker

Steatonyssus aelleni Radovsky & Yunker, 1963. J. Parasit., **49,** 337, figs. 28–33.

The female and protonymph of this species were adequately described by Radovsky & Yunker (1963). The male is unknown.

The female of this species is very close to *S. natalensis* Zumpt & Patterson, differing only in certain of its measurements and in having the antero-dorsal spur of coxa II with a broad, flattened, serrate tip.

Podonotal shield 320μ long, 250μ wide between setae *z3*. Length of setae *i2* equal to two-thirds the distance between setae *i4* and *z2*. Opisthonotal shield 390μ long, 195μ wide at level of setae *J1*. Length of seta *J2* approximately one-third the distance between *J2* and *J3*. Sternal shield 55μ long, 138μ wide between second pair of setae. Chaetotaxy of legs typical for the genus. Length of tibia I, 90μ ; tarsus I, 156μ ; tibia IV, 96μ ; tarsus IV, 180μ ; basal width of tarsus IV, 40μ.

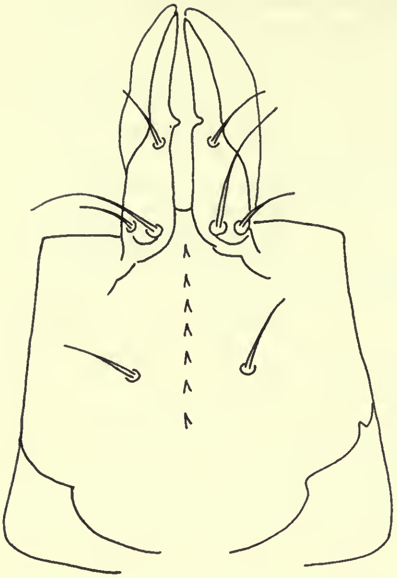
Host and *Locality : Rhinolophus foxi* Thomas from the Cameroons (holotype lent by U.S. National Museum).

Steatonyssus (Steatonyssus) afer Radovsky and Yunker

Steatonyssus afer Radovsky & Yunker 1963, J. Parasit., **49** : 335, figs. 10–16.

FEMALE. Deutosternum has 7 teeth arranged in a single file. Basal segment of chelicera 30μ, second segment 90μ, chelae 40μ long.

Podonotal shield 276μ long, 216μ wide between setae *z3*, bearing eleven pairs of setae. Setae *i2* slightly shorter than, and setae *i4* one and a half times the distance between *i4* and *z2*. Seta *i2* about two-thirds the length of *i3* ; seta *i3* about three-quarters the length of *z1* ; setae *i5* and *z3* subequal. Opisthonotal shield concave anteriorly, 330μ long, 180μ wide at level of setae *J1*, bearing 7 pairs of setae. Terminal setae longer than the subterminals but shorter than the postero-lateral setae. Length of seta *J2* about three-quarters the distance between *J2* and *J3*. Both shields are reticulate.



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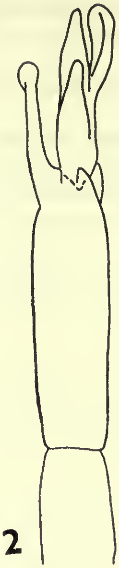

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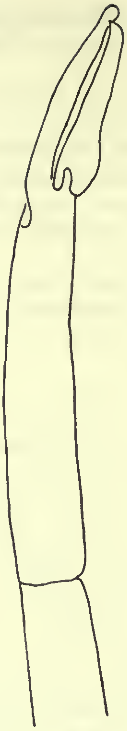

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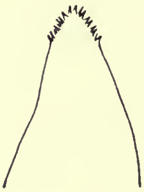

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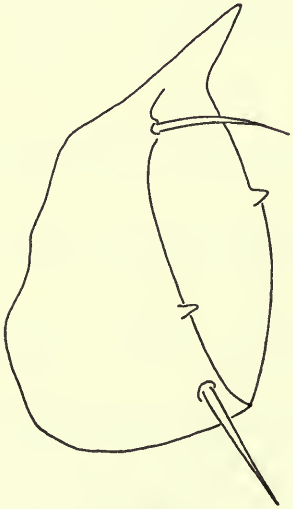

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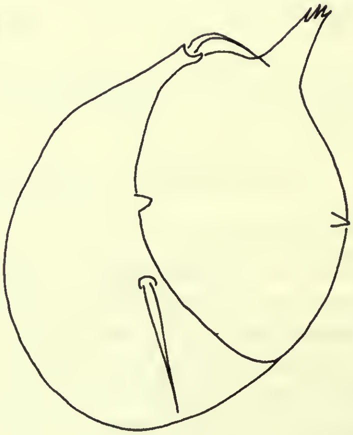


5b

Figs. 1–4. *Steatonyssus* (*Steatonyssus*) *periblepharus* Kolenati. Gnathosoma of female (fig. 1) ; chelicera of male (fig. 2) ; chelicera of female (fig. 3) ; tectum (fig. 4).
Figs 5a–b. *Steatonyssus* (*Steatonyssus*) *brucei* Lavoipierre. Coxa II in different positions.

Sternal shield not sharply demarcated from reticulate presternal area, lateral margins indistinct, posterior region heavily sclerotized. Length of shield about 57μ, width between second pair of setae 110μ. First sternal seta about three-quarters the length of the second and a little more than half as long as the third. Genital shield 144μ long from level of genital setae, 75μ wide between the setae ; length of genital setae about three-quarters the distance between their bases. Anal shield 120μ long to base of postanal seta, 80μ wide through middle of anus. Paranal setae near posterior margin of anus, about four-fifths as long as postanal seta.

Integument of idiosoma bears about 120 pairs of setae ; those on the dorsum and the posterior part of the venter are longer and stouter than the mid-ventral setae. The longest postero-dorsal setae measure 66μ. Peritremes terminate at a point a little beyond the anterior margin of coxa III in the paratype examined, and to the posterior fourth of coxa II in the specimens from Sierra Leone. The peritrematal shield is interrupted, the separated anterior part lying over coxae I and II. Small endopodal shields are present between coxae III and IV and a pair of weakly sclerotized metapodal shields is situated behind coxae IV.

Chaetotaxy of the legs follows the typical *Steatonyssus* pattern. Coxa II bears a sharply pointed antero-dorsal spine. In a specimen from Sierra Leone, in which the second coxa is distorted in position, the spine appears to have a serrated margin with 4 tiny denticles. Length of tibia I, 87μ ; tarsus I, 135μ ; tibia IV, 90μ and tarsus IV, 170μ ; basal width of tarsus IV, 40μ.

MALE. Basal segment of chelicera 24μ, second segment 63μ, spermadactyl 36μ long. Dorsal shield 504μ long, 192μ wide between setae *z*3, bearing 19 pairs of setae. The shield has a reticulate pattern, except on the posterior tip, which is striated.

Holoventral shield narrow, reticulate, bearing 3 pairs of sternal setae, one pair of genitals, 8 ventral setae and 3 anals. The metasternal setae are situated on the striated integument beside the holoventral shield.

Integument of idiosoma bears 45 pairs of setae similar in appearance to those on the female. Peritremes terminate slightly behind the anterior margin of coxa III ; peritrematal shield extends to posterior fourth of coxa II. Endopodal shields are present at the level of coxae IV and a pair of weakly sclerotized metapodal shields is situated behind coxae IV.

Chaetotaxy of legs as in the female ; anterior seta of coxa III has an anterior, plate-like extension of the basal two-thirds. Length of tibia I, 70μ ; tarsus I, 112μ ; tibia IV, 66μ, and tarsus IV, 117μ.

PROTONYMPH. Not known.

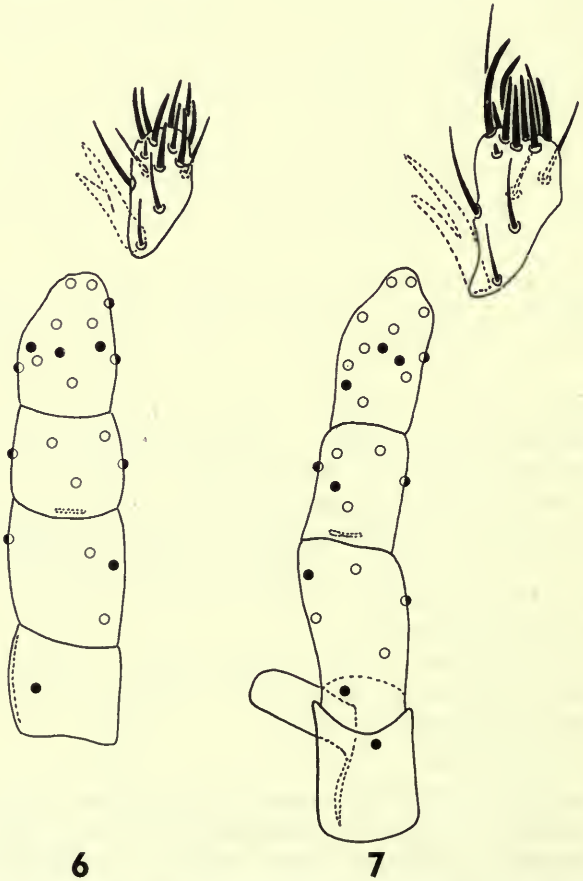
HOSTS AND LOCALITIES. *Nycteris macrotis* Dobson from Lunda, Dundo, Angola (1 ♀ paratype presented by Dr. F. Radovsky). Mixed collection of *Eptesicus tenuipinnis* (Peters) and *Pipistrellus nanus* (Peters), Lunda, Dundo, Angola (1 ♂ paratype presented to B.M.N.H.). Radovsky & Yunker (1963) have recorded one female paratype from the latter host. " Small bat ", Njala, Sierra Leone, collected by E. Hargreaves. [Material in British Museum (Natural History).]

Steatonyssus (Steatonyssus) antrozoi Radovsky & Furman

Steatonyssus antrozoi Radovsky & Furman 1963, Ann. ent. Soc. Amer. **56** : 269, figs. 1–7, 9, 16, 19–21.

Female. Deutosternum has 8 teeth arranged in a single file. Basal segment of chelicera 40μ, second segment 108μ, chela 50μ long.

Podonotal shield 300μ long, 250μ wide between setae *z3*. It bears eleven pairs of setae, *i2* being about two-thirds as long as *i3* ; the lengths of setae *i4* and *z2* are approximately equal to the distance between their bases. Seta *i3* about three-quarters as long as *z1*, setae *i5* and *z3* subequal. Opisthonotal shield concave anteriorly, 354μ long, 186μ wide at the level of setae *J1*. The shield bears 6 pairs of setae, the three posterior pairs being minute. Length of seta *J2* slightly less than half the distance between the bases of *J2* and *J3*. Both shields are reticulate, the opisthonotal shield having longitudinal striations near its tip.



Figs. 6–7. *Steatonyssus* (*Steatonyssus*) *periblepharus* Kolenati. Right pedipalp of protonymph (dorsal view) with tarsus (ventral view), fig. 6 ; right pedipalp of female (dorsal view) with tarsus (ventral view), fig. 7.

Sternal shield 48μ long, 114μ wide between setae II. Anterior part of shield reticulate, not sharply demarcated from the reticulate presternal area ; posterior portion thickened and granular in appearance. Sternal seta I is three-quarters as long as seta III and the same length as seta II. Genital shield 144μ long from level of genital setae, 60μ wide between the setae. Length of genital setae slightly less than the distance between their bases. Anal shield 114μ long to base of postanal seta, 80μ wide through middle of anus. Paranal setae level with posterior fourth of anus, approximately the same length as the postanal seta.

Integument of idiosoma bears about 95 pairs of setae. The ventral ones are slender, finely tapering, the dorsal ones are thicker, tapering near their tips ; those near the posterior end of the body are the thickest and have a maximum length of 45μ. The peritreme extends approximately to the posterior third of coxa II. The separated, anterior, leaf-like part of the peritrematal shield lies on the dorsum and extends from the middle of coxa II to the middle of coxa I. Endopodal shields are present between coxae III and IV ; one pair of roughly oval metapodal shields is situated behind coxae IV.

Chaetotaxy of the legs typical for the genus. Coxa II has a long, pointed, antero-dorsal spine. Length of tibia I, 84μ ; tarsus I, 150μ ; tibia IV, 90μ ; tarsus IV, 168μ ; basal width of tarsus IV, 45μ.

MALE. Basal segment of chelicera 30μ, second segment 66μ, spermadactyl 48μ long. Dorsal shield 528μ long, 210μ wide between setae *z*3 ; it is reticulate anteriorly, striate posteriorly, and bears 18 pairs of setae, the three posterior pairs being very minute.

Holoventral shield reticulate anteriorly, striate posterior to the genital setae, bearing 4–8 setae in the preanal region. The metasternal setae are situated on the integument beside the shield. Integument of idiosoma bears about 52 pairs of setae. Peritreme extends to posterior fourth of coxa II ; endo- and metapodal shields as in the female.

Chaetotaxy of legs as in the female. Anterior seta of coxa III with an anterior expansion near its base. Length of tibia I, 70μ ; tarsus I, 120μ ; tibia IV, 72μ, and tarsus IV, 114μ.

PROTONYMPH. Podontal shield 192μ long, 132μ wide between setae *z*3. Pygidial shield 42μ long, 105μ wide. It bears a pair of relatively short anterior setae and two pairs of longer and stouter posterior setae. The subterminal setae are absent as in the female. Two pairs of mesonotal scutellae are present at the level of setae *J*1–*J*2. Anal shield 40μ long to base of postanal seta, 50μ wide through middle of anus. Integument of venter bears 5 pairs of setae in addition to the genitals.

Chaetotaxy of the legs normal. Posterior setae on coxae II and III inflated basally ; distal antero-dorsal seta on femur IV stouter than any of the other leg setae. Length of tibia I, 36μ ; tarsus I, 60μ ; tibia IV, 42μ, and tarsus IV, 72μ.

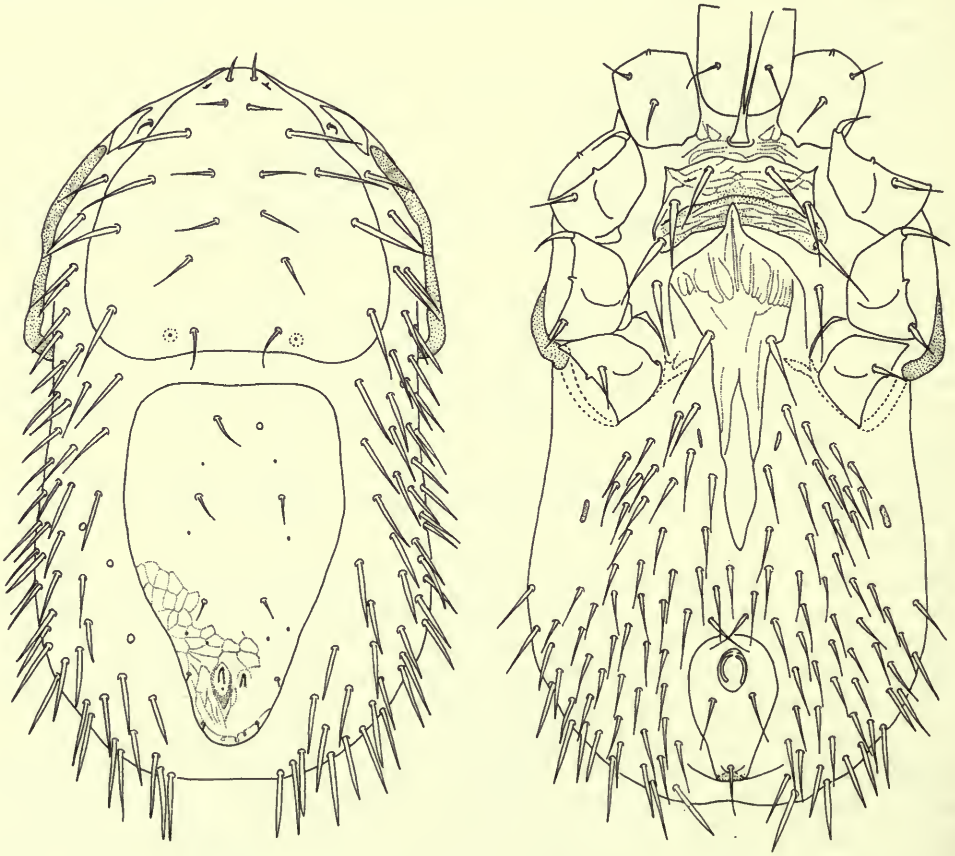
HOSTS AND LOCALITIES. *Antrozous pallidus pacificus* Merriam from Capay, Yolo Co., California, U.S.A. (Two male, 4 female and 2 protonymphal paratypes presented to B.M.N.H.) *Eptesicus fuscus* (Palisot de Beauvois), Oklahoma and Texas, U.S.A. (recorded by Radovsky & Furman, 1963).

Steatonyssus benoiti sp. nov.

FEMALE (Text-figs. 8–9). Deutosternum has 9 teeth. Basal segment of chelicera 30–33μ long, second segment 105–108μ, chelae 33μ long.

Podontal shield 264–288μ long, 234–258μ wide between setae *z*3. Setae *i*2 absent, seta *i*3 approximately half as long as *z*1. Length of setae *i*4 and *z*2 slightly less than the distance between their bases ; seta *i*5 about half as long as *z*3. Opisthonotal shield 324–350μ long, 186–210μ wide at the level of setae *J*1. It bears 5 pairs of setae, both the terminals and subterminals being absent. Length of seta *J*2 less than a quarter the distance between *J*2 and *J*3. Both shields have a reticulate pattern.

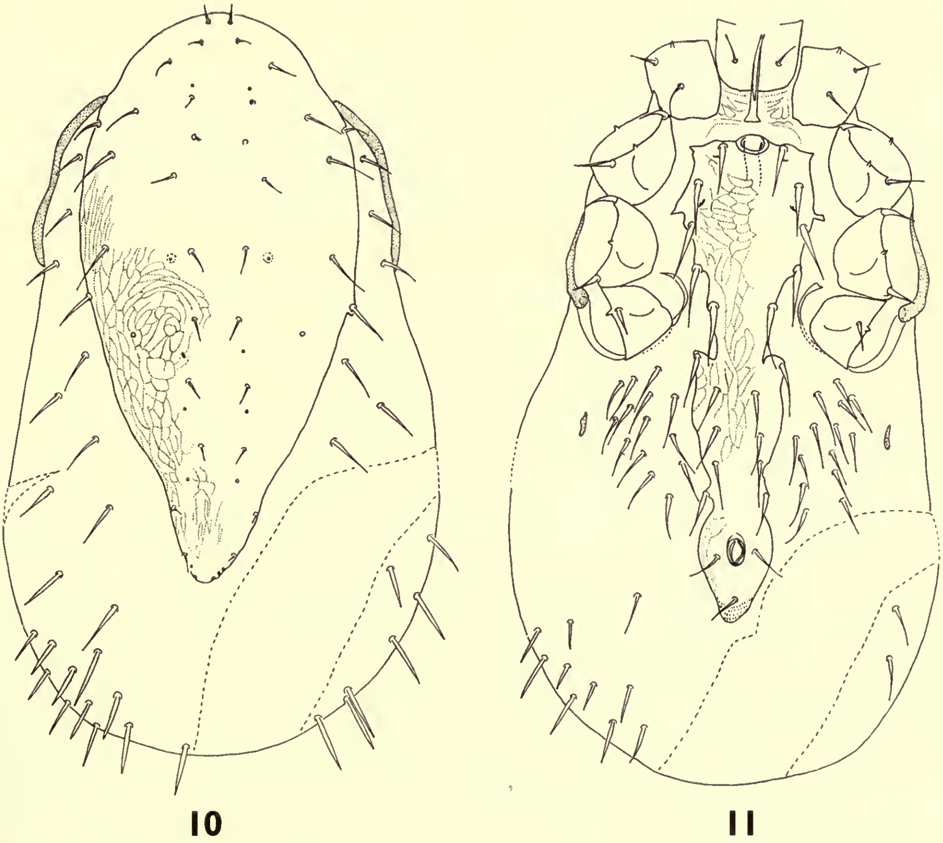
Sternal shield not very sharply demarcated from the reticulate presternal area ; length 60–63μ, width between setae II 123–132μ. The posterior part of the shield



FIGS. 8–9. *Steatonyssus* (*Steatonyssus*) *benoiti* sp. nov. Dorsum (fig. 8) and venter (fig. 9) of female.

is more heavily sclerotized than the anterior part ; the reticulations are more narrowly spaced in the posterior region and there appears to be some granulation. The sternal and metasternal setae are subequal in length. Genital shield relatively long and narrow, with a rather broad antero-median projection extending over the sternal shield. Length from level of genital setae 190–207µ, width between the setae 50–60µ ; length of genital setae about one and a half times the distance between their bases. Anal shield 123–129µ long to base of postanal seta, 78–84µ wide through middle of anus.

Integument of idiosoma bears numerous setae. The ventral ones are inflated basally, tapering rapidly to form long, slender points ; the marginal and dorsal ones taper more gradually and have a maximum length of 66µ. Peritremes long and relatively broad ; they curve onto the dorsum and terminate at a point level approximately with the middle of coxa II. The peritrematal shield is interrupted and the anterior leaf-like portion lies over coxae I and II. Endopodal shields are



FIGS. 10–11. *Steatonyssus* (*Steatonyssus*) *benoiti* sp. nov. Dorsum (fig. 10) and venter (fig. 11) of male.

present between coxae III and IV, and a pair of elongate metapodal shields is situated behind coxae IV.

Chaetotaxy of the legs follows the typical *Steatonyssus* pattern. Coxa II has an antero-dorsal spine and coxae II–IV have slightly curved, sclerotized ridges on the ventral surface. Length of tibia I, 87–93µ ; tarsus I, 150–168µ ; tibia IV, 99–102µ; tarsus IV, 190–204µ ; basal width of tarsus IV, 45µ.

MALE (Text-figs. 10–11). Only one slightly damaged specimen is present, in which the deutosternum is provided with 6 teeth. Dorsal shield entire, reticulate, with 17 pairs of setae, i.e. including two marginal pairs which are not placed on the shield in the female. Length of shield 552µ, width between setae *z*3 is 222µ.

Holoventral shield narrow, reticulate, with 4 pairs of setae in the sternal region, one pair of genitals, 5 pairs in the preanal region, and the usual 3 anal setae. Integument of idiosoma bears 37 pairs of setae, the marginal and dorsal ones tapering more gradually than the ventral ones, as in the female.

Chaetotaxy of the legs as in the female. Length of tibia I, 80µ ; tarsus I, 135µ ; tibia IV, 90µ, and tarsus IV, 153µ.

PROTONYMPH. Not known.

HOSTS AND LOCALITIES. *Rhinolophus landeri lobatus* Peters, collected by N. Leleup from the Grotte Defrenne, Kakontwe, Congo, 19th September, 1948. Holotype (♀), allotype and 12 female paratypes in the Musée royal de l'Afrique Centrale, Tervuren, Belgium. Seven female paratypes (1963.11.11.53–59) in the collection of the British Museum (Natural History), London.

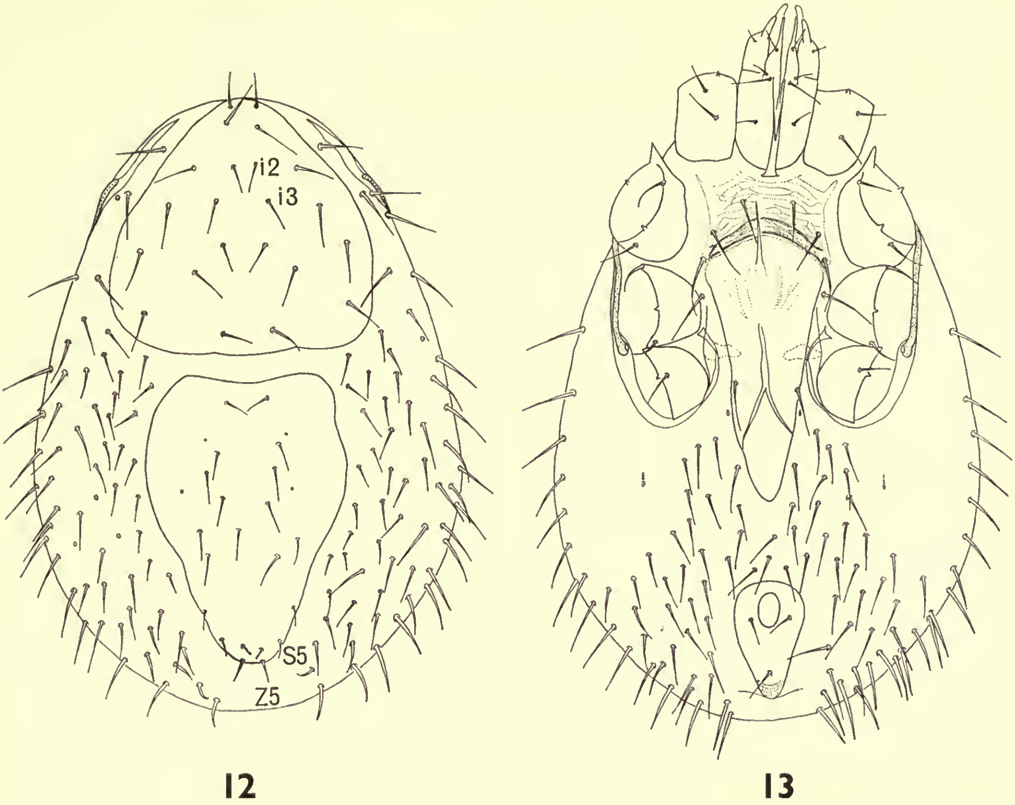
Steatonyssus (Steatonyssus) brucei Lavoipierre

Steatonyssus brucei Lavoipierre 1956, Ann. trop. Med. Parasit. **50** : 295, figs. 3–4.

FEMALE (Text-figs. 12–13). Deutosternum has 7 teeth arranged in a single file. Process on palp trochanter elongate, finger-like. Basal segment of chelicera 27µ, second segment 120µ and chela 42µ long.

Podonotal shield 246–270µ long, 198–210µ wide between setae *z*3, bearing eleven pairs of setae. Setae *i*2–*i*5 subequal, their lengths less than the distance between the bases of setae *i*4 and *z*2. Setae *i*3 and *i*5 are approximately three-quarters the lengths of *z*1 and *z*3 respectively. Opisthonotal shield 270–285µ long, 168–174µ wide at the level of setae *J*1, bearing 20–22 setae which are not all symmetrically arranged. The subterminal setae (*J*5) are about half as long as the terminals (*Z*5). Both shields have a reticulate pattern.

Sternal shield 36–40µ long (from level of setae I), 102µ wide between the second pair of setae. The shield and presternal area are both reticulate and not clearly demarcated from one another. The posterior border of the shield is reticulate and granular and very heavily sclerotized. The sternal setae are more or less subequal in length, the third pair being slightly longer than the first. Genital shield 114–120µ long from the level of the genital setae, 60–66µ wide between the bases of the setae ; length of setae nearly equal to the distance between their bases. The posterior



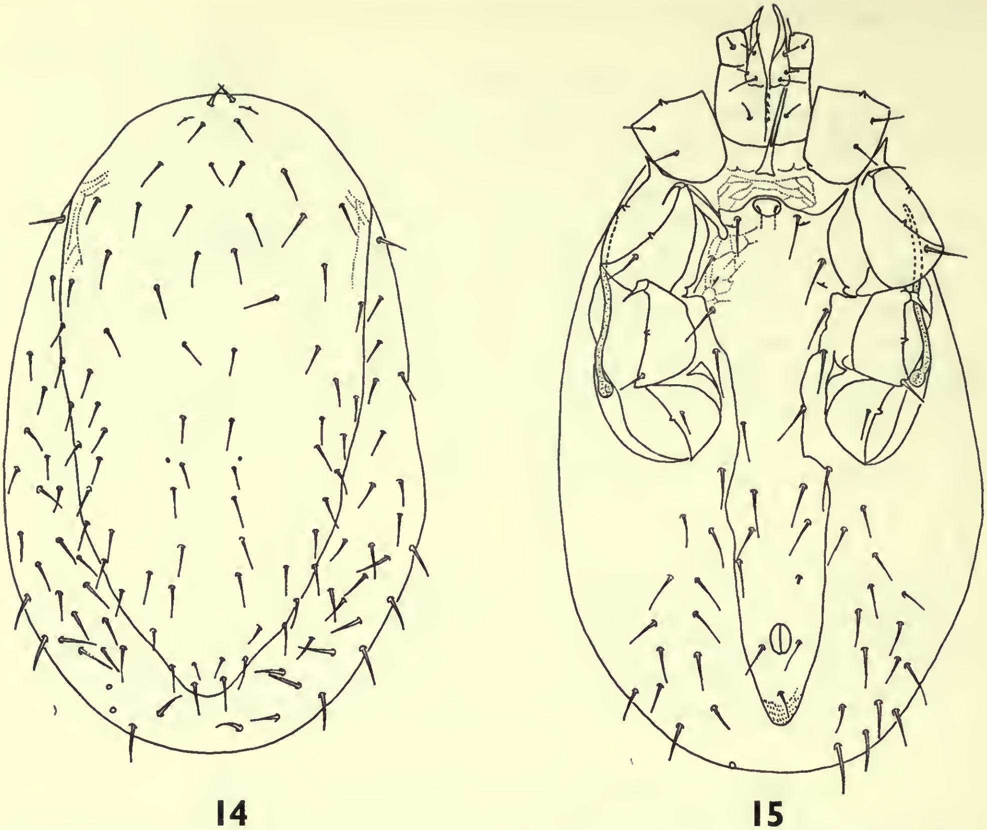
FIGS. 12–13. *Steatonyssus* (*Steatonyssus*) *brucei* Lavoipierre. Dorsum (fig. 12) and venter (fig. 13) of female.

part of the shield bears a pair of well-defined lines which converge near the middle of the shield. Anal shield 90–96μ long to base of postanal seta, 66–70μ wide through middle of anus. Paranal setae a little in front of the posterior margin of the anus.

Integument of idiosoma bears numerous dorsal and ventral setae, those near the margin of the body being relatively stout and spine-like. The postero-dorsal setae have a maximum length of 45μ. Peritremes long, the anterior tips curving onto the dorsum and terminating at a point anterior to the middle of coxa II. The peritrematal shields continue to the middle of coxa I. Endopodal shields present between coxae III and IV and a pair of rather indistinct, oval, metapodal shields is situated behind coxae IV.

The chaetotaxy of the legs follows the typical pattern for this genus. Length of tibia I, 84–87μ ; tarsus I, 150μ ; tibia IV, 75–78μ ; and tarsus IV, 150–165μ ; basal width of tarsus IV, 36μ.

MALE (Text-figs. 14–15). The number of deutosternal teeth cannot be determined. Dorsal shield 414μ long, 144μ wide between setae *z*3, with an overall reticulate



Figs. 14–15. *Steatonyssus* (*Steatonyssus*) *brucei* Lavoipierre. Dorsum (fig. 14) and venter (fig. 15) of male.

pattern. It bears 69 setae ; the lateral ones on the posterior part of the shield are not symmetrically arranged.

Holoventral shield narrow, reticulate, bearing 3 pairs of sternal setae, a pair of genitals, 3 pairs of ventral setae in the preanal region, and the usual 3 anal setae. The metasternal setae are situated on the integument beside the shield.

Integument of idiosoma bears 41 pairs of setae, those near the posterior margin and on the dorsum being relatively stout and spine-like. The peritremes extend to the middle of coxa II. Endopodal shields are present between coxae III and IV and an indistinct, oval, metapodal shield is visible on one side.

Chaetotaxy of the legs as in the female ; anterior seta of coxa III with a projection near its base. Length of tibia I, 60μ ; tarsus I, 99μ ; tibia IV, 57μ ; tarsus IV, 102μ.

Immature stages. Not known.

Hosts and Localities. *Nycteris* spec., Birnim Kebbi, Nigeria (presented by Dr. F. Radovsky). *Pipistrellus nanus* (Peters), Elisabethville, Kipopo, Congo, collected by M. Lips, 1st December, 1955 (sent by Dr. P. L. G. Benoit). *Scotophilus nigrita* (Schreber), Jadotville, Congo, collected by R. P. F. Anciaux de Faveaux, 1st December, 1957 (sent by Dr. P. L. G. Benoit).

Steatonyssus (Steatonyssus) calcaratus Radovsky & Yunker

Steatonyssus calcaratus Radovsky & Yunker 1963, J. Parasit. **49** : 337, figs. 17–27.

Female. Deutosternal teeth not clearly visible in the specimen examined. Basal segment of chelicera 24μ, second segment 80μ, chelae about 36μ long.

Podonotal shield 246μ long, 186μ wide between setae *z*3, bearing eleven pairs of setae. Seta *i*2 very small, approximately half as long as *i*3 and one-third the distance between *i*4 and *z*2. Seta *i*3 about half as long as *z*1, and seta *i*5 nearly as long as seta *z*3. Opisthonotal shield 234μ long, 138μ wide at the level of seta *J*1. It bears 8 pairs of setae and an additional unpaired seta on one side. Setae *J*1 are the longest (24μ) and the 3 posterior pairs are the shortest (12–15μ) ; the subterminal setae are absent. Both dorsal shields have a reticulate pattern.

Sternal shield not very clearly demarcated from the reticulate presternal area ; posterior portion of shield very slightly darker than the anterior portion, with a more compressed reticulate pattern. Length of shield 45μ, width between second pair of setae 108μ. Sternal and metasternal setae subequal in length. Genital shield about 125μ long from level of genital setae, 50μ wide between the setae ; length of setae approximately equal to the distance between their bases. The shield has a slender antero-median process which extends over the sternal shield. Anal shield pear-shaped, 81μ long to base of postanal seta, 60μ wide through middle of anus. Paranal setae level with posterior fourth of anus.

Integument of idiosoma bears about 84 pairs of setae. Ventral setae about 40μ long, slightly inflated basally, tapering to fine points ; dorsal setae shorter and stouter, those near the posterior margin having a maximum length of about 30μ. Peritremes extend beyond middle of coxa II ; peritrematal shields extend to anterior part of coxa I. Endopodal shields are present between coxae III and IV, and a pair of small, very weakly sclerotized metapodal shields is present behind coxae IV.

Chaetotaxy of the legs follows the typical *Steatonyssus* pattern. Coxa III has a pronounced spur which bears the posterior seta near its tip. Length of tibia I, 66μ ; tarsus I, 120μ ; tibia IV, 72μ ; tarsus IV, 140μ ; basal width of tarsus IV, 36μ.

Male. Unknown.

Protonymph. Podonotal shield 156μ long, 102μ wide between setae *z*3, bearing eleven pairs of setae. Pygidial shield about 48μ long, 66μ wide, bearing 3 pairs of setae. The first pair is relatively short, being half as long as the second and three-fifths as long as the third pair. Two pairs of mesonotal scutellae are present at the level of setae *J*1–*J*2. Anal shield 35μ long to base of postanal seta, 42μ wide through middle of anus.

Chaetotaxy of legs normal. Posterior seta of coxa III arises from a small protuberance. Anterior dorsal setae on femur IV stouter than the other leg setae.

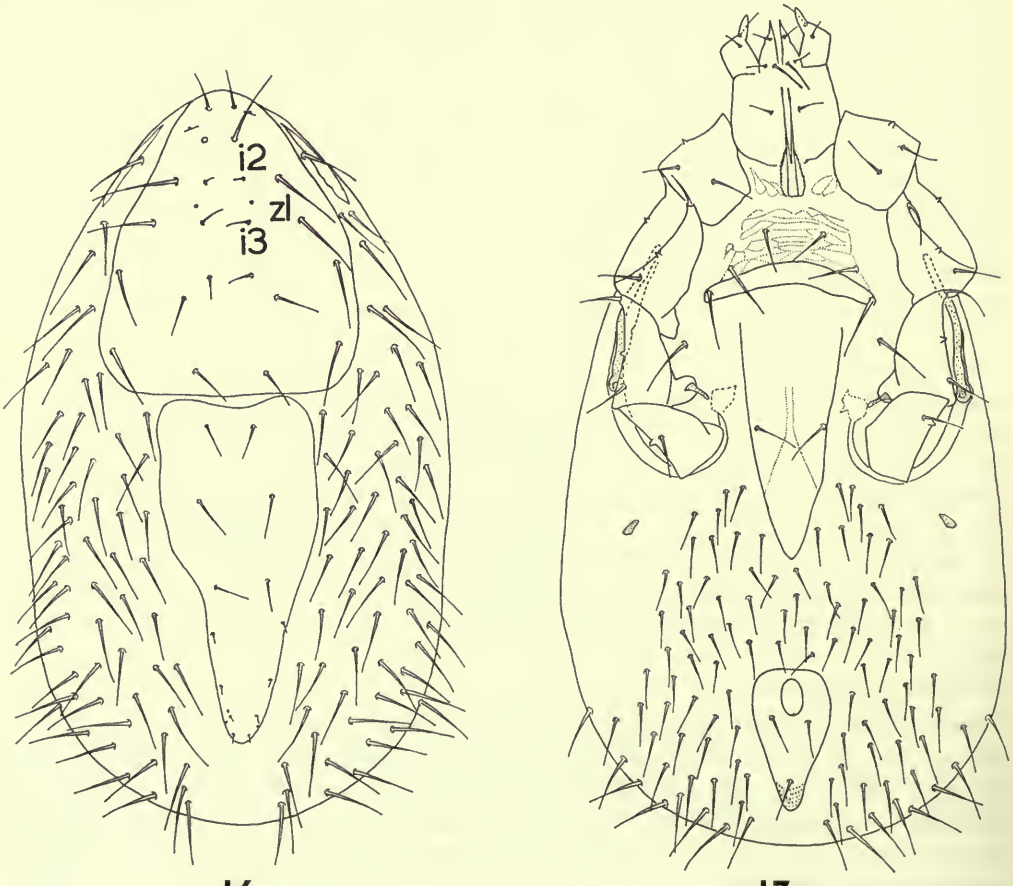
Length of tibia I, 36μ ; tarsus I, 70μ ; tibia IV, 33μ ; tarsus IV, 78μ ; basal width of tarsus IV, 24μ.

HOSTS AND LOCALITIES. *Coleura afra* (Peters), Ngombeni, Kiwali, Kenya, collected by C. E. Yunker, 17th July, 1956 (♀ paratype presented by Dr. F. Radovsky). *Triaenops afer* Peters, Tanga, Sigi River, Tanganyika, collected by C. E. Yunker, 2nd August, 1956 (protonymphal paratype presented by Dr. F. Radovsky).

Steatonyssus (Steatonyssus) ceratognathus (Ewing)

Ceratonyssus ceratognathus Ewing 1923, Proc. U.S. nat. Mus. **62** (2459) : 11–12, pl. 1, fig. 3.
Steatonyssus ceratognathus, Fonseca 1948, Proc. zool. Soc. Lond. **118** : 316 ; Radovsky & Furman 1963, Ann. ent. Soc. Amer. **56** : 274, figs. 13, 17, 23c, 24d.

FEMALE (Text-figs. 16–17). The deutosternal teeth are not clearly visible in the specimens examined. Basal segment of chelicera is 30μ, second segment 100μ and chela 40μ long.



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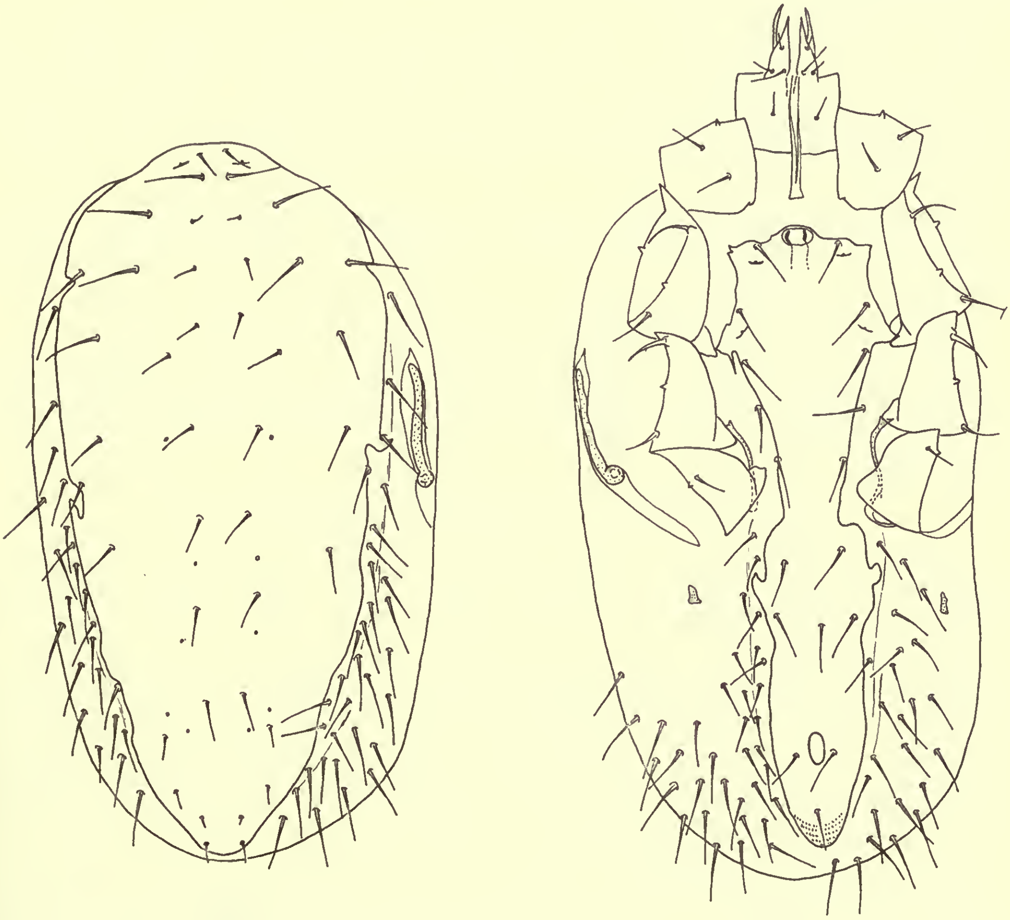
FIGS. 16–17. *Steatonyssus* (*Steatonyssus*) *ceratognathus* (Ewing). Dorsum (fig. 16) and venter (fig. 17) of female.

Podonotal shield 265–274μ long, 214μ wide between setae *z*3, bearing eleven pairs of setae. The setae of the *i* series are relatively short, especially *i*2, which are less than one-third the length of *i*3 ; seta *i*3 is less than one-third as long as *z*1 and seta *i*5 is half as long as seta *z*3. Opisthonotal shield 246–296μ long, 140–164μ wide at the level of setae *J*1, bearing 7 pairs of setae. The length of seta *J*2 is less than half the distance between *J*2 and *J*3, and the 4 posterior pairs of setae are very minute. Both shields have a weakly defined reticulate pattern.

Sternal shield reticulate, posterior portion heavily sclerotized, slightly concave, sternal seta I slightly shorter than seta II. Length of shield 56–63μ, width between second pair of setae 104–120μ. Genital shield 113–126μ long from level of genital setae, 56–63μ wide between the setae ; length of setae about two-thirds the distance between their bases. Anal shield 78–101μ long to base of postanal seta, 66–73μ



FIGS. 18–19. *Steatonyssus* (*Steatonyssus*) *ceratognathus* (Ewing). Dorsum (fig. 18) and venter (fig. 19) of male.

wide through middle of anus. Anus situated very near anterior margin of shield ; paranal setae near posterior margin of anus, slightly more slender than postanal seta but about the same length.

Integument of idiosoma bears numerous setae. Those on the ventral surface are slender and about as long as the genital setae ; the marginal and dorsal setae are about one and a half times as long and stout as the ventral setae, and have a maximum length of 60μ. Peritremes extend to middle of coxa II and are completely separated from the anterior part of the peritrematal shield. A pair of endopodal shields is situated between coxae III and IV, and a pair of roughly elliptical metapodal shields behind coxae IV.

The chaetotaxy of the legs follows the typical *Steatonyssus* pattern. Length of tibia I, 68–82μ ; tarsus I, 136μ ; tibia IV, 74–82μ ; and tarsus IV, 130–158μ ; basal width of tarsus IV, 45μ.

MALE (Text-figs. 18–19). Deutosternal teeth indistinct ; basal segment of chelicera 22μ, second segment 63μ, spermadactyl 42μ long, Dorsal shield 478μ long, 170μ wide between setae *z*3, bearing 20 pairs of setae. Holoventral shield narrow, bearing 17 setae, sternal seta IV being off the shield on one side. Chaetotaxy of integument similar to that of female ; peritremes reach anterior margin of coxa III.

Chaetotaxy of the legs similar to that of the female. Anterior seta on coxa III inflated basally. Length of tibia I, 60μ ; tarsus I, 99μ ; tibia IV, 57μ ; tarsus IV, 105μ.

PROTONYMPH. Described by Radovsky & Furman (p. 274, figs. 17, 23c).

HOSTS AND LOCALITIES. " Bat ", Butesburg, U.S.A., 30th May, 1914 (♀ cotype received on loan from U.S. National Museum). *Nycticeius humeralis* (Rafinesque), Columbia, South Carolina, U.S.A., 15th August, 1960 (1 ♂, 1 ♀ lent by Dr. F. Radovsky).

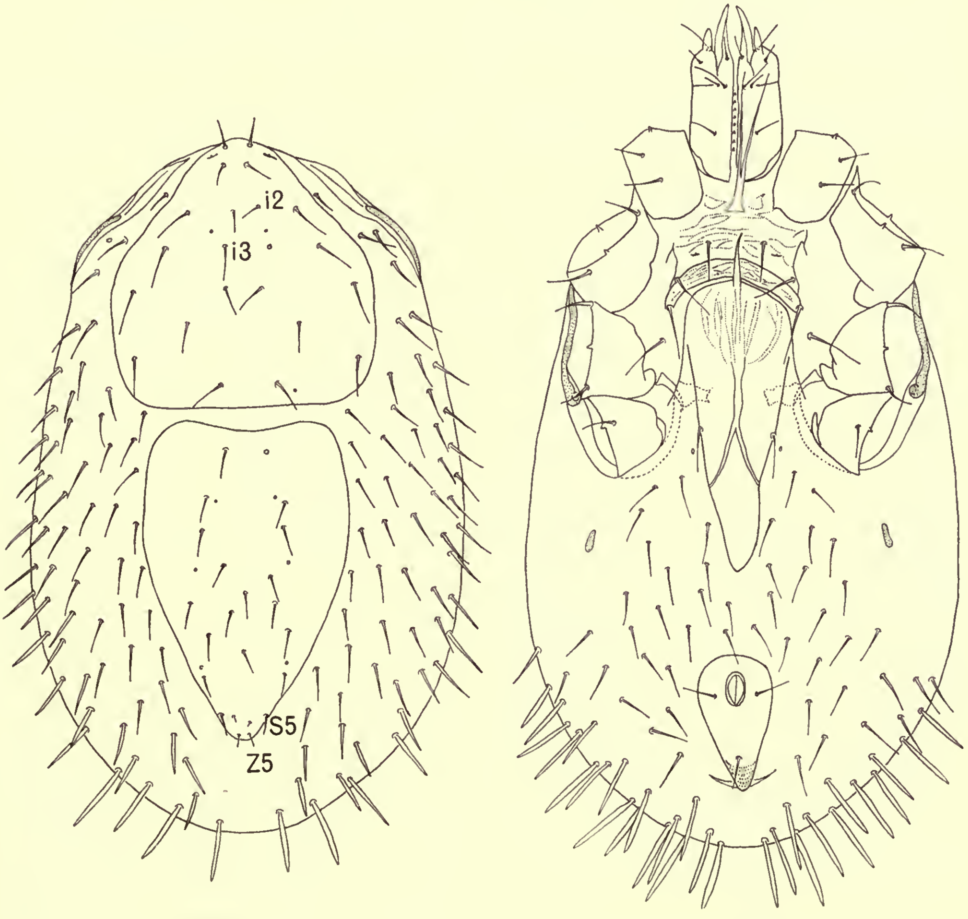
Steatonyssus (Steatonyssus) crassisetosus sp. nov.

FEMALE (Text-figs. 20–21). Deutosternum provided with 8 teeth arranged in a single file. Basal segment of chelicera 27–30μ long, second segment 108–114μ, chelae about 40μ long.

Podonotal shield 246–252μ long, 210–216μ wide between setae *z*3, bearing eleven pairs of setae (seta *i*3 is missing on one side in the holotype). Length of seta *i*2 is less than half the distance between *i*4 and *z*2, and about three-quarters the length of seta *i*3 ; setae *i*3 and *i*5 are three-quarters the lengths of *z*1 and *z*3 respectively. Opisthonotal shield 234–288μ long, 165–180μ wide at the level of setae *J*1, bearing 23 setae. The terminal setae (*Z*5) are slightly shorter than the postero-lateral setae on the shield. Both dorsal shields are reticulate.

Anterior part of sternal shield weakly reticulate, not sharply demarcated from the reticulate presternal area. Posterior portion strongly sclerotized, deeply concave. Length of shield 45–50μ (36–42μ from level of seta I), width between setae II is 105–108μ. Sternal setae I and II subequal in length and about two-thirds as long as setae III and IV. Genital shield bears a pair of strongly sclerotized converging lines and has a pointed antero-median process which extends over the sternal shield. Length of shield from level of genital setae is 130–138μ, distance between the setae is 63–75μ. Length of setae about three-fifths the distance between their bases. Anal shield pear-shaped. Length to base of postanal seta 93–102μ, 72μ wide through middle of anus. Paranal setae on a level slightly behind middle of anus, approximately the same length as the postanal seta.

Integument of idiosoma bears about 103 pairs of setae. The ventral setae are fine and slender, the marginal ones broad and rod-like, tapering only at the extreme tips, and the dorsal ones are rather stiff and spine-like. The postero-dorsal rod-like setae have a maximum length of 75μ. Peritremes long, curving onto the dorsum and terminating over the anterior part of coxa II; the peritrematal shields continue to the anterior fourth of coxa I. Endopodal shields present between coxae III



FIGS. 20–21. *Steatonyssus* (*Steatonyssus*) *crassisetosus* sp. nov. Dorsum (fig. 20) and venter (fig. 21) of female.

and IV and a pair of roughly oval metapodal shields is present behind coxae IV.

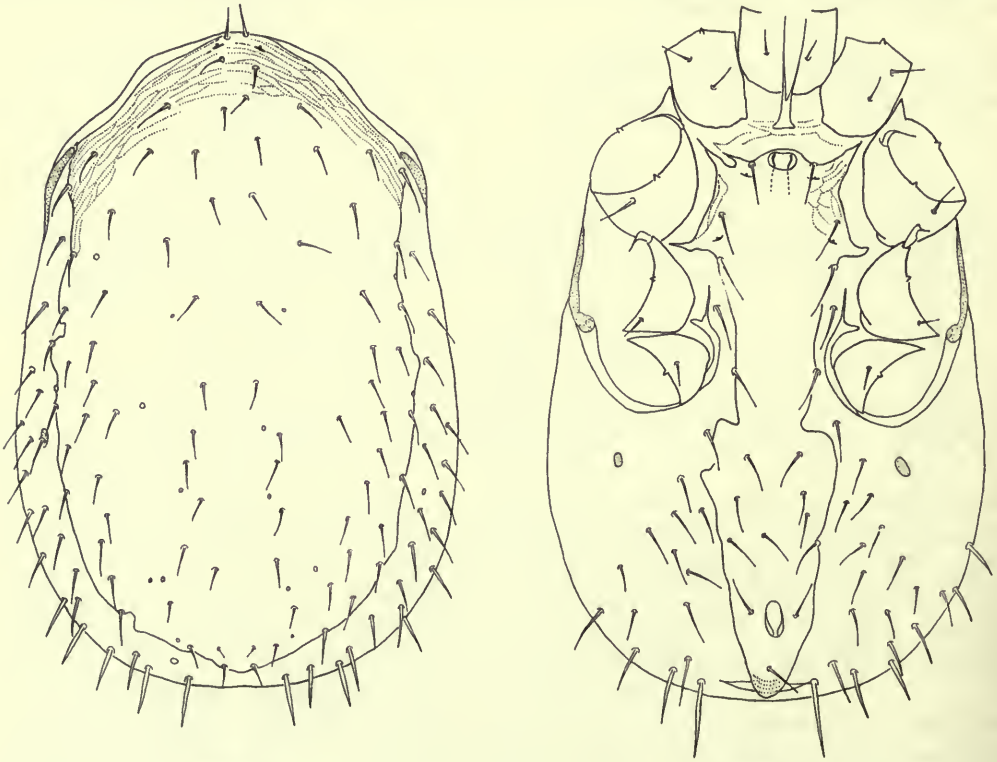
Chaetotaxy of the legs follows the typical *Steatonyssus* pattern. Length of tibia I, 90μ ; tarsus I, 160μ ; tibia IV, 84μ, and tarsus IV, 165–170μ ; basal width of tarsus IV, 40μ.

MALE (Text-figs. 22–23). Deutosternum bears 8 teeth. Basal segment of chelicera 24μ, second segment 66μ, chela with spermadactyl 40μ long.

Dorsal shield entire and covers almost the whole dorsum. Its length is 438–474μ; its width between setae *z*3 is 174–180μ. The shield incorporates many more setae than in the female, but the number is variable in different specimens and even on different sides of the same specimen. The number of setae on the anterior part of the shield (15 pairs) appears to be constant, whereas on the posterior part the number on each side may vary between 23 and 28 setae.

The holoventral shield has irregular lateral margins. It bears 3 pairs of setae in the sternal region, the metasternals being on the adjacent integument, one pair of genitals, 8–13 setae in the preanal region, and the usual 3 anal setae.

The setae on the unsclerotized integument are similar in form to those of the female. Peritremes extend to middle of coxa II ; endo- and metapodal shields



22 **23**

FIGS. 22–23. *Steatonyssus* (*Steatonyssus*) *crassisetosus* sp. nov. Dorsum (fig. 22) and venter (fig. 23) of male.

as in the female. Chaetotaxy of the legs as in the female. Anterior seta on coxa II inflated basally and terminating in a lateral point. Length of tibia I, 70μ ; tarsus I, 123–126μ ; tibia IV, 65–70μ ; tarsus IV, 110–126μ.

PROTONYMPH. Not known.

HOSTS AND LOCALITIES. *Tadarida spillmanni* Monard, Kinke, Elisabethville, Congo, collected by Messrs. Anciaux and Lips, 23rd December, 1955 (material sent by Dr. V. Aellen). Holotype (1963.11.11.39), allotype (1963.11.11.44), two male (1963.11.11.42–43) and two female paratypes (1963.11.11.40–41) in the collection of the British Museum (Natural History) ; two male and four female paratypes presented to the Muséum d'Histoire naturelle, Geneva ; one male and one female paratype presented to the South African Institute for Medical Research, Johannesburg.

Steatonyssus (Steatonyssus) emarginatus Radovsky & Furman

Steatonyssus emarginatus Radovsky & Furman 1963, Ann. ent. Soc. Amer. **56** : 270, figs. 15, 22, 24c, 25.

FEMALE. Deutosternum has 7 teeth arranged in a single file. Basal segment of chelicera 21μ, second segment 90μ, chelae 27μ long.

Podonotal shield 243μ long, 198μ wide between setae *z*3, bearing 12 pairs of setae. In one of the specimens examined a 13th seta appears to be situated on the extreme margin on one side of the shield. Setae *i*2 are extremely minute, about one-fifth the length of *i*3 ; seta *i*3 is about two-thirds as long as *z*1 and seta *i*5 is nearly as long as *z*3. Opisthonotal shield 294μ long, 130μ wide at the level of setae *J*1. It bears 7 pairs of setae. The three anterior pairs are relatively long (about 45μ) ; length of seta *J*2 about half the distance between *J*2 and *J*3. The posterior setae are short and fine (12–18μ) ; the terminal pair is the longest and the subterminal pair is extremely minute. Both shields are reticulate, except the posterior tip of the opisthonotal shield, which bears longitudinal striations.

Sternal shield 50μ long, 110μ wide between setae II. Anterior part of shield reticulate ; posterior part thickened, with a finely granular appearance and a few reticulations. Sternal seta I about seven-eighths as long as seta II. Genital shield 120μ long from the level of the genital setae, 78μ wide between the setae ; length of genital setae slightly more than half the distance between their bases. Anal shield 94μ long to base of postanal seta, 70μ wide through middle of anus. Paranal setae situated near posterior margin of anus, slightly shorter than the postanal seta.

Integument of idiosoma bears numerous setae ; the ventral ones are slender and hair-like, becoming stouter towards the posterior margin ; the dorsal setae are a little longer and thicker than the ventral ones, those near the posterior margin having a maximum length of 50μ. Peritreme does not reach anterior margin of coxa III. The separated, leaf-like, anterior portion of the peritrematal shield lies over the anterior half of coxa II and the posterior half of coxa I. A pair of indistinct metapodal shields is situated behind coxae IV.

Chaetotaxy of the legs typical for the genus. Coxa II has a long, pointed, anterodorsal spine. Length of tibia I, 75μ ; tarsus I, 123μ ; tibia IV, 75μ ; tarsus IV, 135μ ; width of tarsus IV, at the base, 39μ.

MALE AND PROTONYMPH. Described by Radovsky & Furman (p. 272).

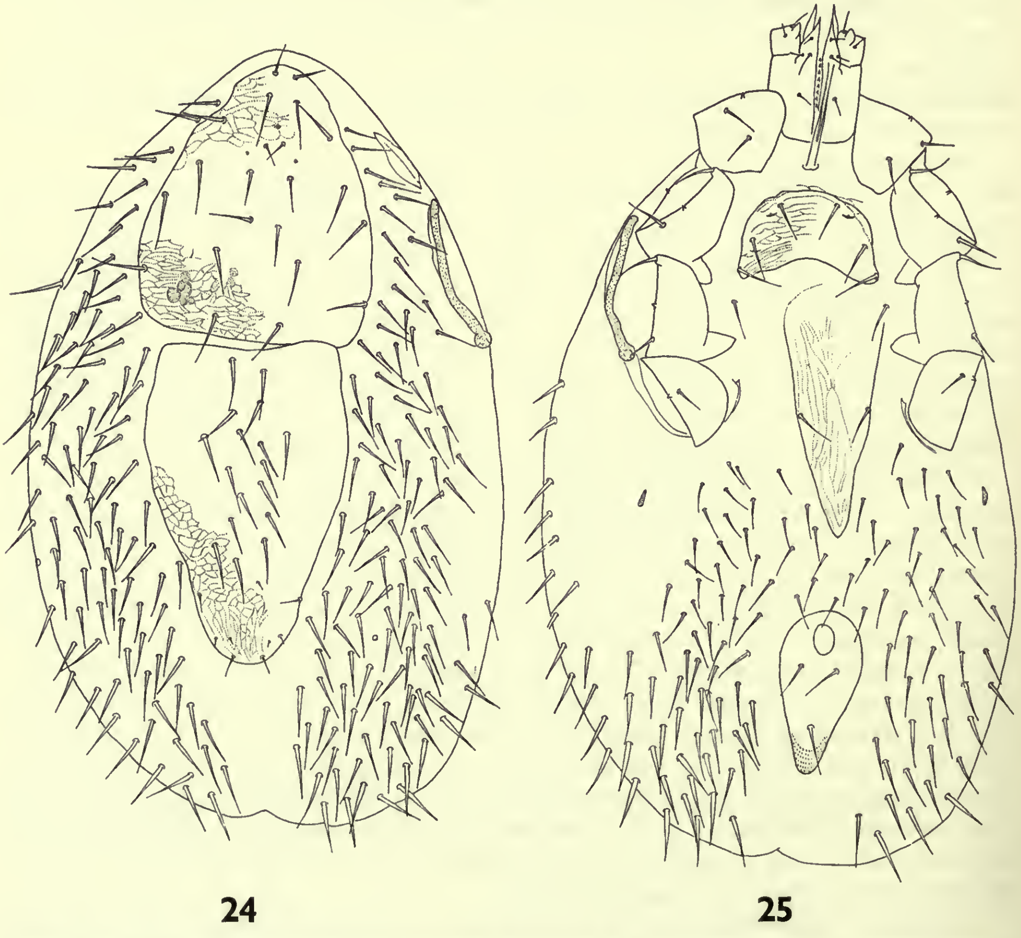
HOSTS AND LOCALITIES. *Pipistrellus hesperus* (H. Allen), Sabins Canyon, Santa Catalina Mountains, Arizona, U.S.A. (2 ♀♀, presented by Dr. F. Radovsky).

Radovsky & Furman (1963) list this species from the same host in California, and also from the following hosts and localities: *Myotis yumanensis* (H. Allen), Justiceburg, Garza Co., Texas. *Myotis* spec., Madera Co., California, U.S.A.

Steatonyssus (Steatonyssus) eos Zumpt & Till

Steatonyssus eos Zumpt & Till 1954, J. ent. Soc. S. Afr. **17** : 55, figs. 3–4.

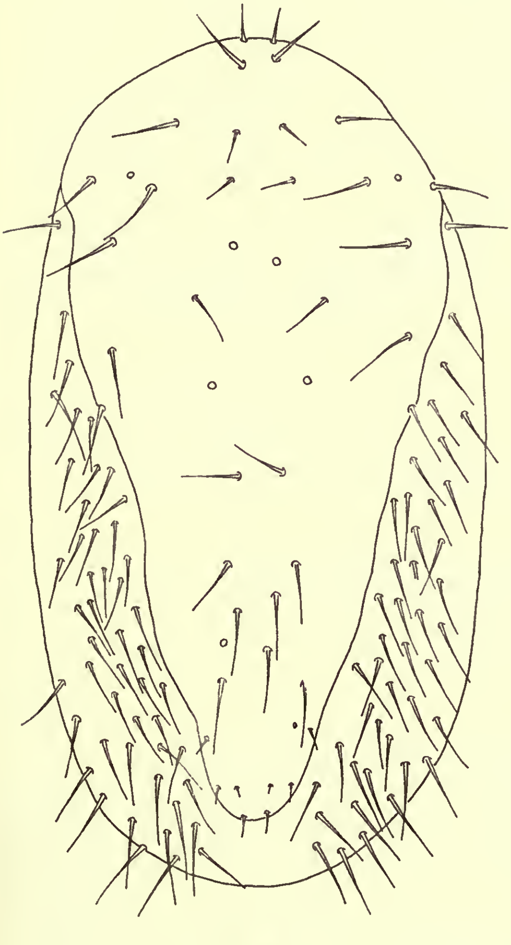
FEMALE (Text-figs. 24–25). Deutosternum with 8 teeth arranged in a single file. First cheliceral segment 24μ, second segment 80μ, chelae 40μ long.



FIGS. 24–25. *Steatonyssus (Steatonyssus) eos* Zumpt & Till. Dorsum (fig. 24) and venter (fig. 25) of female.

Podonotal shield 315–318µ long, 240–242µ wide between setae *z*3, bearing eleven pairs of setae. Length of seta *i*2 about three-fifths the length of *i*3, and less than half the distance between *i*4 and *z*2 ; seta *i*3 about two-thirds as long as *z*1 ; setae *i*5 and *z*3 subequal. Opisthonotal shield 354–357µ long, 204–210µ wide at the level of setae *J*1. It bears 23–26 setae, not all symmetrically placed. The anterior ones are relatively long and stout ; the four pairs of posterior setae, and in one specimen an additional unpaired seta, being relatively short and fine. The subterminals are minute. Both shields are strongly reticulate.

Sternal shield convex anteriorly, concave posteriorly, faintly granular in appearance and with a reticulate pattern which is more compressed on the posterior part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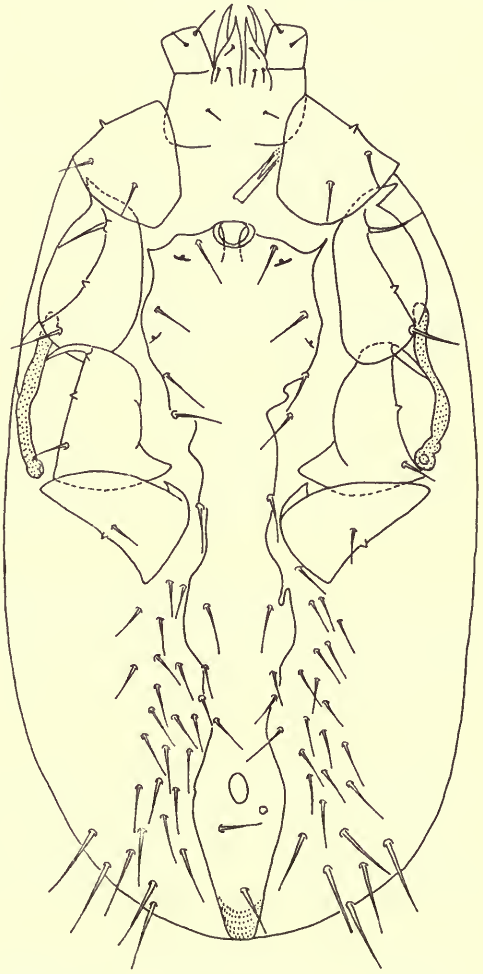
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FIGS. 26–27. *Steatonyssus* (*Steatonyssus*) *eos* Zumpt & Till. Dorsum (fig. 26) and venter (fig. 27) of male.

of the shield. Length of shield 66–72μ, width between second pair of setae 132–138μ. Sternal and metasternal setae subequal in length. Genital shield with linear markings, 138–144μ long from level of genital setae, 78μ wide between the setae ; length of setae little more than half the distance between their bases. Anal shield an elongate pear shape, 132–156μ long to base of postanal seta, 90μ wide through middle of anus. Paranal setae situated posterior to the anus, slightly shorter and more slender than the postanal seta.

Integument of idiosoma bears numerous setae, the medially placed ventral ones being relatively short and slender, the marginal and dorsal ones being longer and stouter, with a maximum length of 66μ. Peritremes extend to the middle of coxa II and are widely separated from the anterior part of the peritrematal shield. Endo- and metapodal shields are not clearly visible in these specimens.

Chaetotaxy of the legs typical for the genus. Length of tibia I, 80μ ; tarsus I, 126μ ; tibia IV, 90μ ; tarsus IV, 165μ ; basal width of tarsus IV, 42μ.

MALE (Text-figs. 26–27). Deutosternum with 7 teeth. Basal segment of chelicera 30μ, second segment 70μ, chela with spermadactyl 45μ long. Dorsal shield strongly reticulated, 582μ long, 228μ between setae *z*3. The shield bears 21 pairs of setae, the 4 posterior pairs being very short and fine.

Holoventral shield very narrow, reticulate, with irregular margins. Metasternal setae present, one being off the shield. Integument of idiosoma with numerous setae of a similar form to those in the female. Peritremes extend almost to middle of coxa II.

Chaetotaxy of legs as in the female ; coxa III has a stout spine-like, anterior seta. Length of tibia I, 72μ ; tarsus I, 110μ ; tibia IV, 80μ ; tarsus IV, 135μ.

HOSTS AND LOCALITIES. *Pipistrellus nanus* (Peters) from Muhoroni, Kenya, 22nd December, 1952 [paratypes in the British Museum (Natural History)].

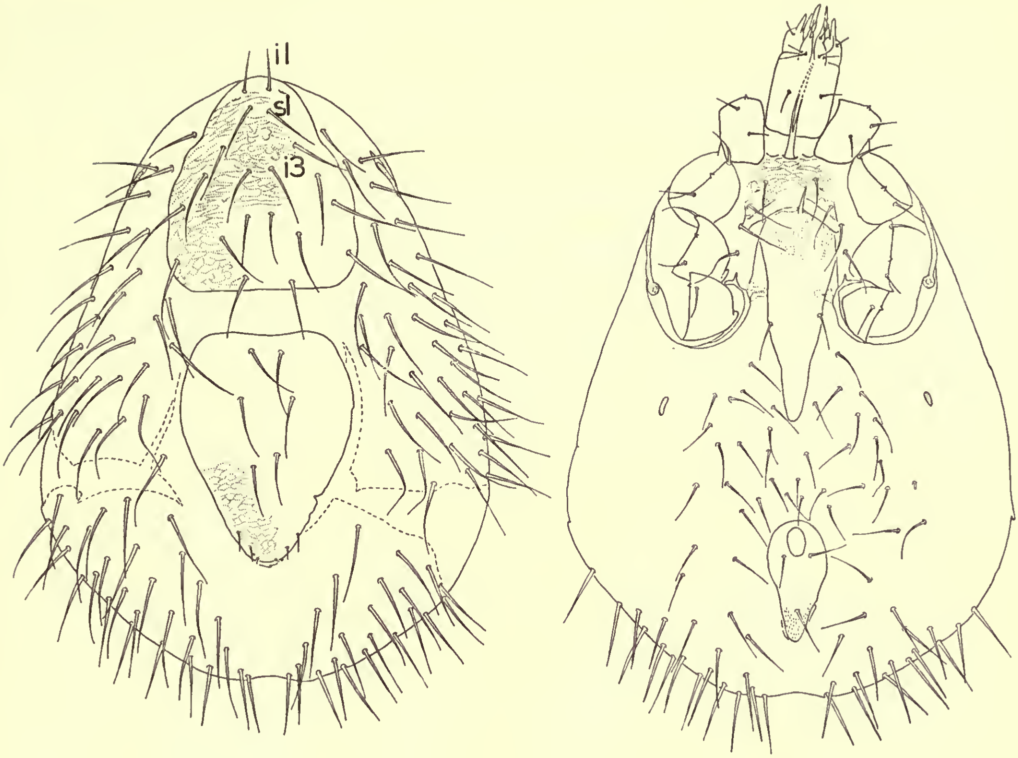
Steatonyssus (Steatonyssus) evansi Delfinado

Steatonyssus evansi Delfinado 1960, Fieldiana, Zoology **42** : 107, figs. 38 A, B.
Steatonyssus primus Grokhovskaya & Nguen-Huan-Hoe 1961, Zool. Zh. Moscow **40** : 1,565 & 1,641 (syn. nov.).

FEMALE (Text-figs. 28–29). Deutosternal teeth not clearly visible. Chela 50μ long, basal cheliceral segment 36–42μ, second segment 130–148μ long.

Podonotal shield 270–337μ long, 252–277μ between setae *z*3, bearing 10 pairs of setae. Setae *i*2 missing ; seta *i*3 nearly as long as *z*1 ; seta *i*5 about three-quarters as long as *z*3. Opisthonotal shield 306–365μ long, 222–227μ wide at the level of setae *J*1, bearing 6 pairs of setae. Setae *J*1–*J*3 are relatively long, the length of *J*2 being approximately equal to the distance between *J*2 and *J*3. The 3 posterior pairs are less than one-third the length of *J*2 ; setae *Z*5 are extremely small. Both shields have a well marked reticulate pattern.

Sternal shield about 50μ long (from level of seta I), 114–126μ wide between second pair of setae. The posterior portion is slightly thickened in appearance but does



28 **29**

Figs. 28–29. *Steatonyssus* (*Steatonyssus*) *evansi* Delfinado. Dorsum (fig. 28) and venter (fig. 29) of female.

not form a heavily chitinized band. Sternal setae I and II subequal in length. Genital shield 144–158μ long from level of genital setae, 72–82μ wide between the setae ; length of setae about half the distance between their bases. Anal shield pear-shaped, 114–145μ long to base of postanal seta, 87–88μ wide through middle of anus. Paranal setae near posterior margin of anus, slightly shorter than postanal setae.

Integument of idiosoma bears numerous setae. There are about 20 pairs of slender ventral setae. Near the posterior margin the setae are broad, blade-like, tapering at the extreme tips. On the dorsum the setae are longer, coarser, and taper gradually. Peritremes do not quite reach middle of coxa II. Endopodal shields are present between coxae III and IV ; the metapodal shields are oval and weakly sclerotized.

Chaetotaxy of the legs typical for the genus. Length of tibia I, 132–145μ ; tarsus I, 222–252μ ; tibia IV, 132–145μ ; tarsus IV, 240–265μ.

Male. Described by Delfinado (p. 107).

Protonymph. Unknown.

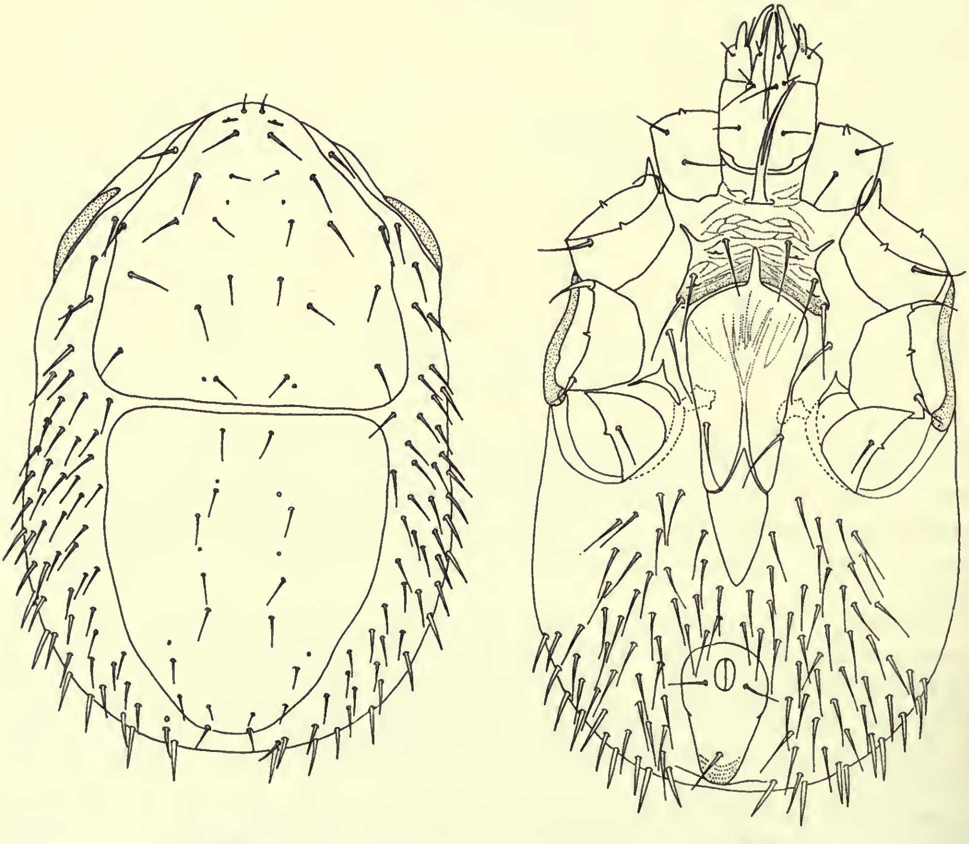
HOSTS AND LOCALITIES. *Scotophilus temminckii* (Horsfield), Mindanao, Philippines (♀ paratype lent by U.S. National Museum). " Bat ", Hanoi, N. Vietnam (♀ examined by courtesy of Dr. N. G. Bregetova). Grokhovskaya & Nguen-Huan-Hoe (1961) record the following hosts from N. Vietnam : *Cynopterus sphinx* (Vahl) ; *Scotophilus kuhli* Leach.

Steatonyssus (Steatonyssus) faini Delfinado

Steatonyssus faini Delfinado 1960, Fieldiana, Zoology **42** : 106, figs. 37 A, B.
Steatonyssus secundus Grokhovskaya & Nguen-Huan-Hoe 1961, Zool. Zh. Moscow **40** : 1,565 & 1,641 (syn. nov.).

FEMALE (Text-figs. 30–31). Deutosternum with 6 teeth. Basal segment of chelicera 18μ, second segment 102μ, chela 33μ long.

Podonotal shield 246–265μ long, 204–220μ between setae *z*3, bearing 12 pairs of setae. Seta *i*2 about three-quarters as long as *i*3 ; setae *i*3 and *i*5 about two-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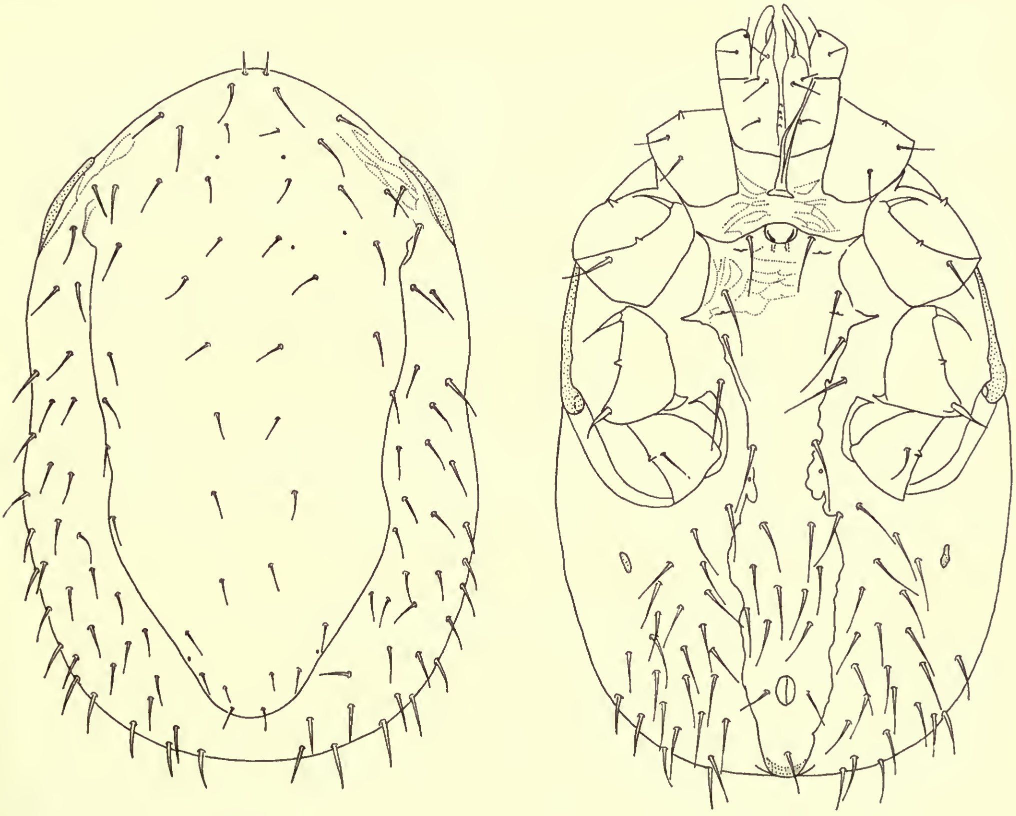
FIGS. 30–31. *Steatonyssus* (*Steatonyssus*) *faini* Delfinado. Dorsum (fig. 30) and venter (fig. 31) of female.

thirds the length of $z1$ and $z3$ respectively. Opisthonotal shield 258–265μ long, 222–235μ wide at the level of setae $J1$, bearing 15–17 setae. Both shields have a reticulate pattern.

Sternal shield 33μ long from level of setae I, 48μ from anterior margin of reticulate area, 96–99μ wide between setae II. Anterior part of shield not clearly demarcated from reticulate presternal area ; posterior portion has a faintly granular appearance and a more compressed reticulate pattern, but it is not heavily sclerotized. Genital shield 109–126μ long from level of genital setae, 55–57μ wide between the setae ; length of setae a little less than the distance between their bases. The shield is marked by a pair of thick, curved lines which converge posterior to the genital setae. Anal shield 84–90μ long to base of postanal seta, 62–70μ wide through middle of anus. Paranal setae near posterior margin of anus, slightly shorter than postanal seta.



32 33

FIGS. 32–33. *Steatonyssus* (*Steatonyssus*) *faini* Delfinado. Dorsum (fig. 32) and venter (fig. 33) of male.

Integument of idiosoma bears about 100 pairs of setae. The ventral ones are long and finely pointed ; those near the posterior margin are relatively stouter, and the dorsal ones are relatively shorter. Peritremes terminate over a point between the middle and anterior margin of coxa II ; peritrematal shield forms a leaf-like expansion which extends nearly to the anterior border of coxa I. A pair of endopodal shields is present between coxae III and IV, and a pair of weakly sclerotized, elongate, metapodal shields is situated behind coxae IV.

Chaetotaxy of the legs typical for the genus. Setae on coxa III stouter than those on the other coxae. Coxae II–IV have curved ridges ventrally. Length of tibia I, 57–58μ ; tarsus I, 94–96μ ; tibia IV, 60–62μ ; tarsus IV, 124–132μ.

MALE (Text-figs. 32–33). Basal segment of chelicera 15μ, second segment 63μ, chela and spermadactyl 40μ long. Dorsal shield 420μ long, 174μ wide between setae *z*3. It bears 22 pairs of setae and two additional marginal setae on one side. There is a reticulate pattern on the antero-lateral part of the shield, but only occasional faint markings can be seen on the remaining part of the shield (in the one specimen available).

Holoventral shield narrow, irregular in outline, with a reticulate pattern. The metasternal setae are situated on the integument beside the shield. The preanal region of the shield bears 4 pairs of setae plus 2 asymmetrically placed marginal ones. Integument of idiosoma bears about 54 pairs of dorsal and ventral setae which are similar in form to those of the female. Endopodal shields level with coxae IV ; metapodal shields as in female ; peritremes extend to anterior part of coxa II.

Chaetotaxy of legs as in female. Anterior seta on coxa II and both setae on coxa III relatively broad basally. Length of tibia I, 45μ ; tarsus I, 75μ ; tibia IV, 48μ ; tarsus IV, 84μ.

PROTONYMPH. Unknown.

HOSTS AND LOCALITIES. *Scotophilus temminckii* (Horsfield), Palawan, Cuyo Island, Philippines (♀ paratype lent by U.S. National Museum). " Bat ", Hanoi, N. Vietnam (♂ and ♀ examined by courtesy of Dr. N. G. Bregetova). Grokhovskaya & Nguen-Huan-Hoe (1961) record the following hosts from N. Vietnam : *Cynopterus sphinx* (Vahl) ; *Scotophilus kuhli* Leach.

Steatonyssus (Steatonyssus) hipposideros Till

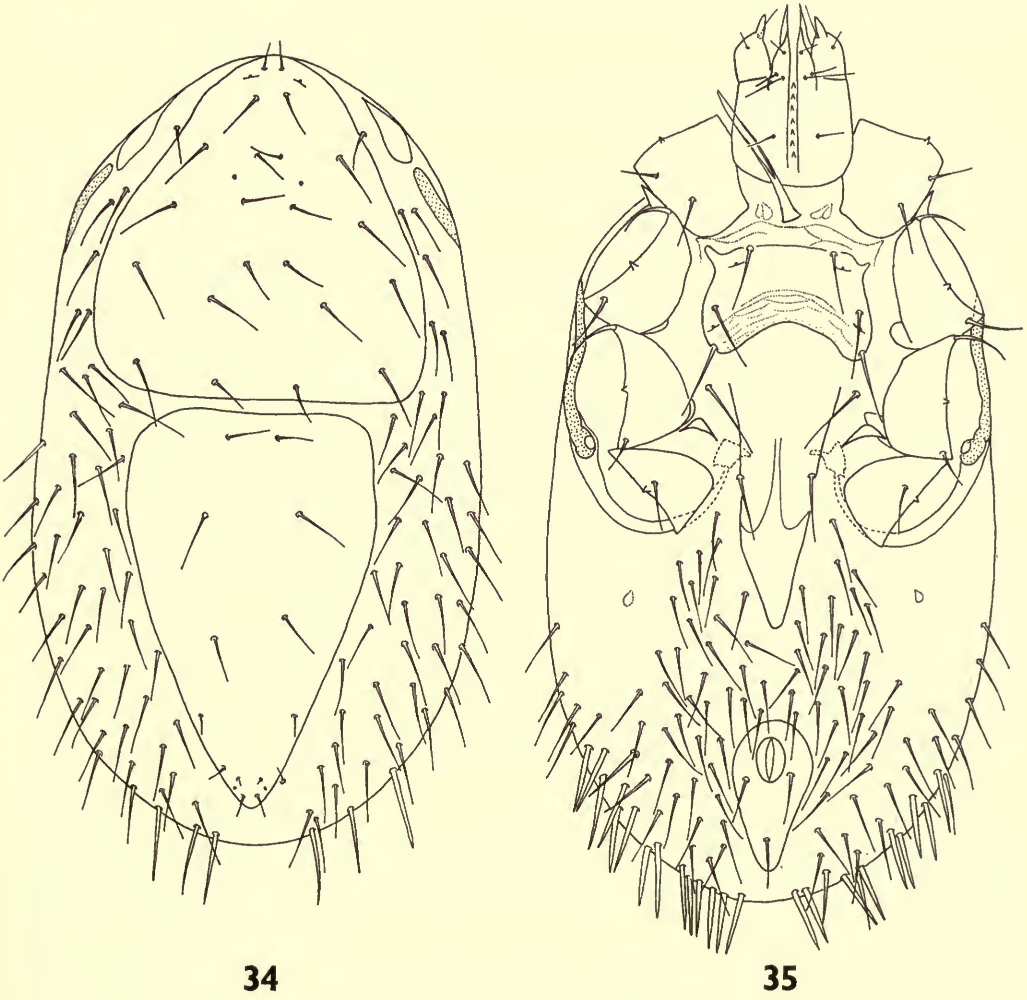
Steatonyssus hipposideros Till 1958, Rev. suisse Zool., **65** : 242, figs. 1–4.

FEMALE (Text-figs. 34–35). Deutosternum has 8 teeth. Basal segment of chelicera 24–30μ, second segment 96μ, chelae 36–40μ long.

Podonotal shield 276–280μ long, 198–204μ wide between setae *z*3, with eleven pairs of setae. Setae *i*2 about five-sixths the length of *i*3, slightly shorter than the distance between *i*4 and *z*2 ; seta *i*3 about two-thirds as long as *z*1 ; seta *i*5 about three-fifths as long as *z*3. Opisthonotal shield 288–318μ long, 183–192μ wide at level of setae *J*1, with 7 pairs of setae. Length of seta *J*2 a little more than half the distance between *J*2 and *J*3. The 4 posterior pairs of setae are relatively short and fine ; the terminals are slightly longer than the postero-laterals ; the subterminals are minute. Both shields have a reticulate pattern.

Sternal shield 60–66μ long, 108–120μ wide between setae II. Posterior part of shield has a slightly thickened and granular appearance and a more compressed reticulate pattern than the anterior part of the shield. Sternal seta I about three-quarters the length of seta II. Genital shield 126μ long, 54–60μ wide between the genital setae ; length of setae equal to the distance between their bases. Anal shield pear-shaped, 90–96μ long to base of postanal seta, 63–72μ wide through middle of anus. Paranal setae near posterior margin of anus, about the same length as the postanal seta.

Integument of idiosoma bears numerous setae, including about 40 pairs of hair-like ventral setae. The marginal setae are broad and blade-like, the postero-dorsal

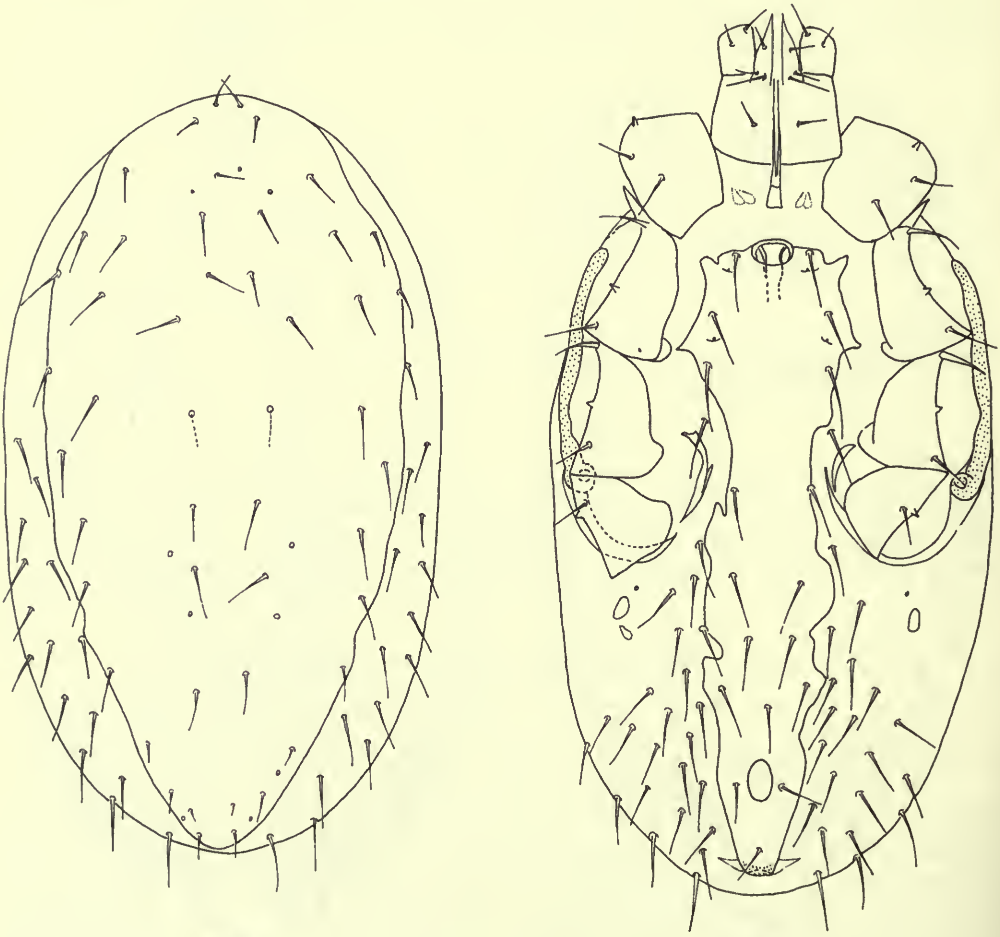


Figs. 34–35. *Steatonyssus* (*Steatonyssus*) *hipposideros* Till. Dorsum (fig. 34) and venter (fig. 35) of female.

ones having a maximum length of about 66μ. Peritremes reach the anterior margin of coxa II ; the separated anterior part of the peritrematal shield lies over coxa I. Endopodal shields are present between coxae III and IV ; the metapodal shields are very weakly sclerotized and irregularly ovoid in shape.

Chaetotaxy of the legs typical for the genus. Length of tibia I, 90μ ; tarsus I, 150μ ; tibia IV, 90μ ; tarsus IV, 168–174μ ; basal width of tarsus IV, 42μ.

Male (Text-figs. 36–37). Deutosternum with 8 teeth ; basal segment of chelicera 24μ, second segment 66μ, chela and spermadactyl 42μ long. Dorsal shield 474–480μ long, 165–174μ wide between setae *z*3, with an overall reticulate pattern and an irregular margin. It bears 26 pairs of setae.



36 **37**

Figs. 36–37. *Steatonyssus* (*Steatonyssus*) *hipposideros* Till. Dorsum (fig. 36) and venter (fig. 37) of male.

Holoventral shield narrow, irregular in outline, with a granular and reticulate pattern. Metasternal setae situated on the integument beside the shield ; from 8–12 setae present in the preanal region of the shield. Setae on the integument of the idiosoma relatively slender, only the terminal pair being noticeably thickened. Peritremes as in the female ; metapodal shields present, variable in shape.

Chaetotaxy of the legs as in the female ; anterior setae on coxae II and III thickened. Length of tibia I, 70µ ; tarsus I, 110µ ; tibia IV, 70µ ; and tarsus IV, 126µ.

PROTONYMPH. Unknown.

HOSTS AND LOCALITIES. *Hipposideros cyclops* (Temminck) from Yapo, Ivory Coast, 14th August, 1953 (2 ♂ and 3 ♀ paratypes lent by Dr. F. Zumpt, South African Institute for Medical Research).

Steatonyssus (Steatonyssus) javensis javensis (Oudemans)

Liponyssus javensis Oudemans 1914, Ent. Ber. Amst. **4** (76) : 69, & 1915, Arch. Naturgesch. Abt. A., **81** (1) : 167, figs. 135–153.

Ceratonyssus javensis, Ewing 1922, Proc. U.S. nat. Mus. **62** : 6.

Steatonyssus javensis, Buitendijk 1945, Overdrukt Zool. Med. **24** : 307 ; Fonesca 1948, Proc. zool. Soc. Lond. **118** : 316.

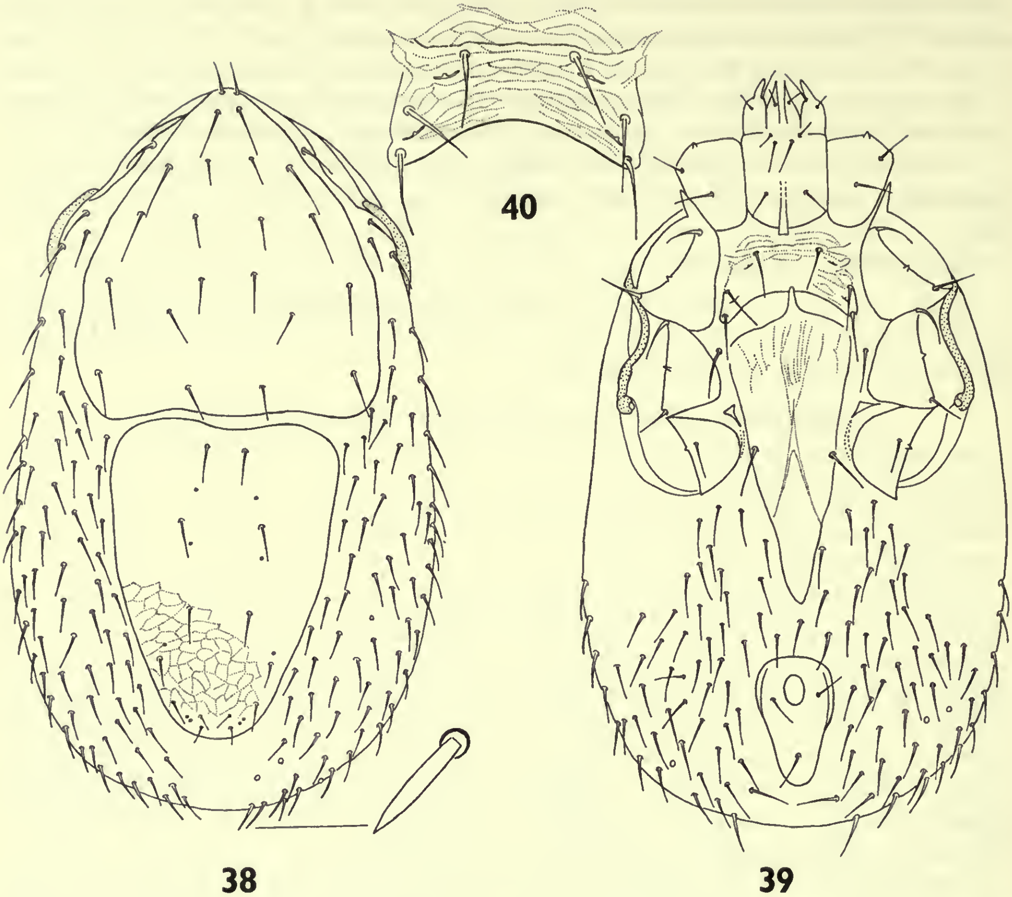
FEMALE (Text-figs. 38–40). Deutosternum with 7 teeth. Basal segment of chelicera 36µ, second segment 105µ, chelae about 30µ long.

Podonotal shield 210–220µ long, 170–177µ wide between setae *z*3, bearing eleven pairs of setae. Lengths of setae *i*2 and *i*3 subequal, three-fifths the distance between *i*4 and *z*2. Seta *i*3 two-thirds as long as *z*1 ; seta *i*5 about three-quarters the length of *z*3. Opisthonotal shield 208–223µ long, 140–156µ wide at the level of setae *J*1, with 7 pairs of setae. Length of seta *J*2 about one-third the distance between setae *J*2 and *J*3 ; terminal setae not longer than the postero-laterals ; subterminals three-quarters as long as the terminals.

Sternal shield concave posteriorly, without any posterior thickening, but with a more compressed reticulate pattern in that region. Length of shield 32–36µ, width between second pair of setae 80–90µ. Sternal and metasternal setae subequal in length. Genital shield 105–108µ long from level of genital setae, 54µ wide between the setae ; length of setae two-thirds the distance between their bases. Anal shield pear-shaped, 66–70µ long to base of postanal seta, 50–54µ wide through middle of anus. Paranal setae near posterior margin of anus, slightly shorter than postanal seta.

Integument of idiosoma bears numerous setae which tend to become shorter and stouter towards the posterior end of the body. The postero-dorsal setae have a maximum length of 27µ. Peritremes reach anterior fourth of coxa II ; peritrematal shields continue to the anterior fourth of coxa I. Endo- and metapodal shields are not clearly visible.

Chaetotaxy of the legs typical for the genus. Coxa II has a large antero-dorsal spine which, in certain positions, appears to have minute terminal denticulations. Length of tibia I, 45µ ; tarsus I, 66µ ; tibia IV, 42µ ; tarsus IV, 78µ ; basal width of tarsus IV, 27µ.

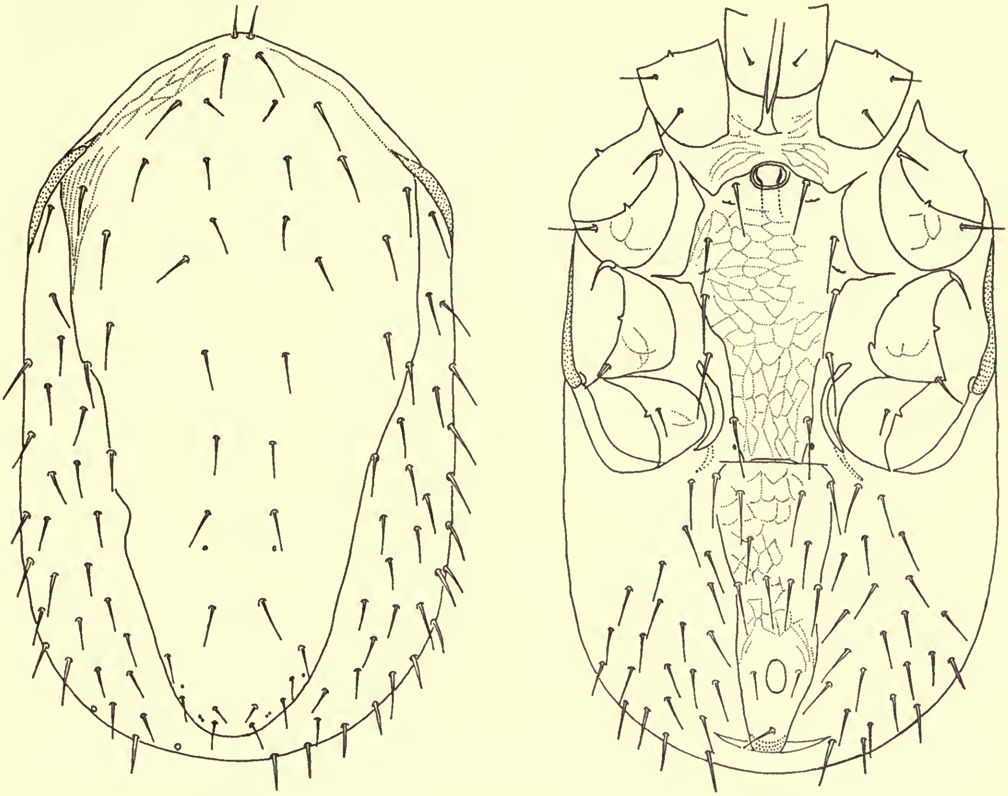


FIGS. 38–40. *Steatonyssus* (*Steatonyssus*) *javensis javensis* (Oudemans). Dorsum with one enlarged seta (fig. 38) ; venter (fig. 39) and enlarged sternal shield (fig. 40) of female.

MALE (Text-figs. 41–42). Deutosternum with 7 teeth. Basal cheliceral segment 15μ, second segment 60μ, chela and spermadactyl 30μ long. Dorsal shield 340–355μ long, 138–144μ wide between setae *z*3. It bears 20 pairs of setae, 12 on the anterior and 8 on the posterior part. The shield has a reticulate pattern anteriorly, but behind setae *z*2 and *z*3 it has a granular appearance.

The sternito-genital shield is separated from the ventri-anal by a suture. The former bears 4 pairs of setae, the metasternals being on the striated integument adjacent to the shield ; the latter bears 5 pairs of setae in the preanal region and the usual 3 anal setae. Integument of idiosoma bears about 50 pairs of setae similar in form to those of the female. Peritremes extend to anterior part of coxa II.

Chaetotaxy of legs as in the female. Length of tibia I, 40μ ; tarsus I, 54μ ; tibia IV, 36μ ; tarsus IV, 63μ.



Figs. 41–42. *Steatonyssus* (*Steatonyssus*) *javensis javensis* (Oudemans). Dorsum (fig. 41) and venter (fig. 42) of male.

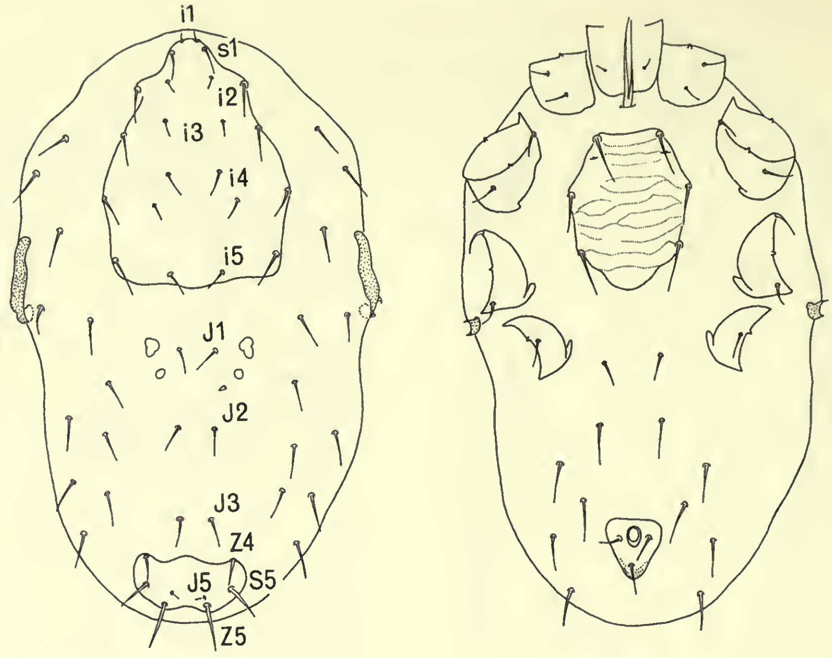
Protonymph (Text-figs. 43–44). Podonotal shield 150μ long, 99μ between setae *z*3. Pygidial shield 33μ long, 66μ wide. It bears 4 pairs of setae, the anterior pair being half as long as the posterior pair ; the subterminal setae are minute. Anal shield 30μ long to base of postanal seta, 36μ wide through middle of anus.

Chaetotaxy of legs normal. Length of tibia I, 27μ ; tarsus I, 39μ ; tibia IV, 24μ ; tarsus IV, 45μ.

Hosts and Localities. " Chiropteron ", Khandala, Bombay, India, 1911 (males, females, protonymphs lent by Dr. L. van der Hammen, Rijksmuseum van Natuurlijke Historie, Leiden). *Pipistrellus babu* Thomas, Sanghu Village, Maewa Khola, Nepal, collected by K. H. Hyatt, 6th March, 1962.

Steatonyssus (Steatonyssus) javensis brevisetosus ssp. nov.

Female (Text-figs. 45–47). Deutosternum bears 6 denticles. Basal segment of chelicera 15μ, second segment 114μ, chelae 33μ long.

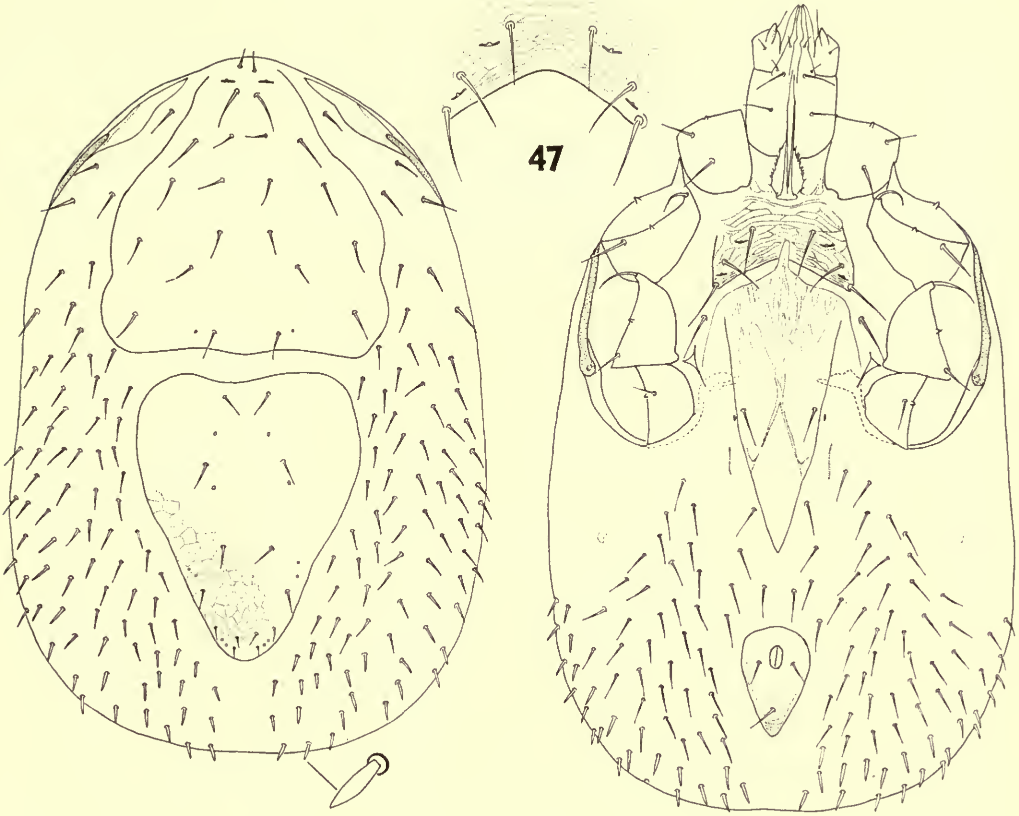


43 44

FIGS. 43–44. *Steatonyssus* (*Steatonyssus*) *javensis javensis* (Oudemans). Dorsum (fig. 43) and venter (fig. 44) of protonymph.

Podonotal shield 228μ long, 168μ wide between setae *z3*, bearing eleven pairs of setae. Lengths of setae *i2* and *i3* subequal, about half the distance between *i4* and *z2* ; seta *i3* about two-thirds the length of *z1* ; seta *i5* about seven-eighths the length of *z3*. Opisthonotal shield 204–228μ long, 156–168μ wide at the level of setae *J1*, bearing 7 pairs of setae. Setae *J1*–*J3* about the same length as those of the *i* series ; length of *J2* less than one-third the distance between *J2* and *J3* ; terminal setae (*Z5*) slightly shorter than the subterminals. Both shields have a reticulate pattern.

Sternal shield reticulate, not demarcated from the reticulate presternal area, lateral margins weakly defined, posterior margin more deeply concave than in *S. javensis javensis*. The posterior part of the shield has a more compressed pattern than the anterior part, but is not heavily sclerotized. Total length of shield about 40μ, length from level of first pair of setae 24–27μ, width between second pair of setae about 90μ. Sternal setae I and II subequal in length. Genital shield 108–111μ long from level of genital setae, 54μ wide between the setae ; length of setae about half the distance between their bases. Anal shield 60–63μ long to base of postanal seta, 51–57μ wide through middle of anus. Paranal setae level with posterior third of anus.



FIGS. 45–47. *Steatonyssus* (*Steatonyssus*) *javensis brevisetosus* ssp. nov. Dorsum with one enlarged seta (fig. 45), venter (fig. 46) and enlarged sternal shield (fig. 47) of female.

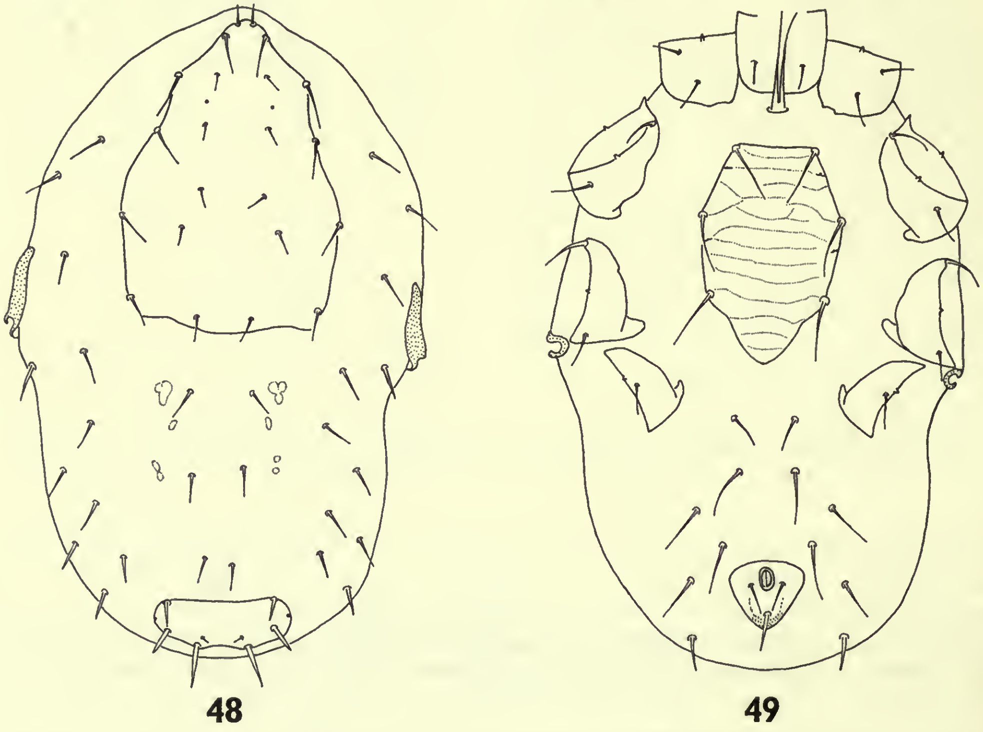
Integument of idiosoma bears numerous setae which become progressively shorter and stouter towards the caudal end of the body. The postero-dorsal setae are relatively shorter than in *S. javensis javensis*, having a maximum length of about 12µ. Peritremes extend to anterior half of coxa II ; peritrematal shields continue nearly to anterior margin of coxa I. Endopodal shields are present between coxae III and IV and a pair of weakly sclerotized metapodal shields is visible behind coxae IV.

Chaetotaxy of the legs typical for the genus. The antero-dorsal spine on coxa II has 2 or 3 minute denticles at its tip. Length of tibia I, 45µ ; tarsus I, 69µ ; tibia IV, 45µ ; tarsus IV, 78µ ; basal width of tarsus IV, 27µ.

MALE. Unknown.

PROTONYMPH (Text-figs. 48–49). Podonotal shield 147–153μ long, 87–93μ wide between setae *z*3, bearing eleven pairs of setae. Pygidial shield 30μ long, 66μ wide, with 3 pairs of relatively stout setae and a pair of minute subterminals. The terminal setae are relatively shorter and stouter than in *S. javensis javensis*. The weakly sclerotized mesonotal scutellae may be subdivided. Anal shield 27μ long to base of postanal seta, 33μ wide through middle of anus.

Chaetotaxy of legs normal. Anterior spine on coxa II appears to have small denticles at its tip. Length of tibia I, 27μ ; tarsus I, 40μ ; tibia IV, 22–24μ ; tarsus IV, 40μ.



FIGS. 48–49. *Steatonyssus* (*Steatonyssus*) *javensis brevisetosus* ssp. nov. Dorsum (fig. 48) and venter (fig. 49) of protonymph.

HOSTS AND LOCALITIES. *Eptesicus tenuipinnis* (Peters), Uvira, Congo, collected by Drs. P. L. G. Benoit & N. Leleup, 2nd March, 1955. Holotype, 1 ♀ paratype and 10 protonymphs in the collection of the Musée royal de l'Afrique centrale, Belgium. Two ♀ paratypes (1963.11.11.60–61) and 3 protonymphs (1963.11.11.62–64) in the collection of the British Museum (Natural History).

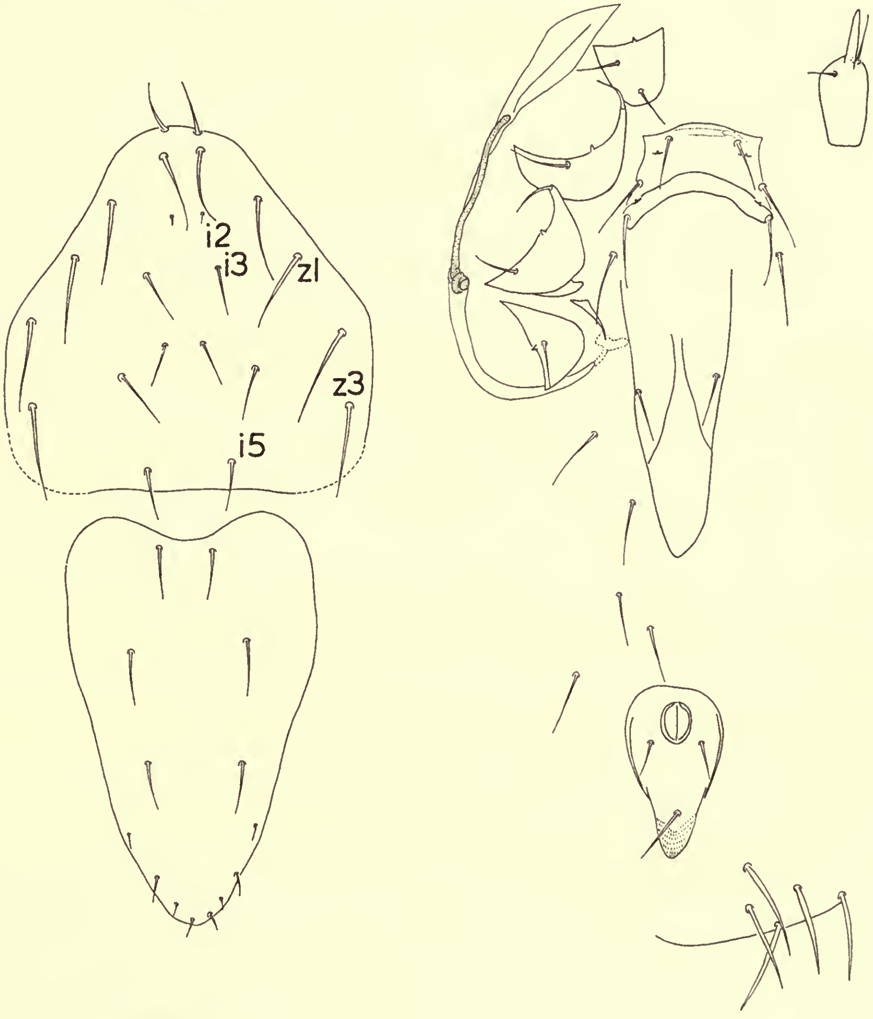
Eidolon helvum (Kerr), Stanleyville, Congo, collected by R. Collart, 2.vii.1929. Twenty-four female paratypes and 5 protonymphs in the collection of the Musée royal de l'Afrique Centrale, Belgium ; twelve female paratypes (1963.11.11.65–74) and 2 protonymphs in the collection of the British Museum (Natural History).

Myotis bocagei (Peters), Bamanya, Congo, collected by R. P. G. Hulstaert, 1956. One ♀, one protonymph in the collection of the Musée royal de l'Afrique centrale, Belgium.

Steatonyssus (Steatonyssus) joaquimi (Fonseca)

Ceratonyssus joaquimi Fonseca 1935, Mem. Inst. Butantan S. Paulo **9** : 89, figs. 1–6.
Steatonyssus joaquimi Fonseca 1948, Proc. zool. Soc. Lond. **118** : 317.

FEMALE (Text-figs. 50–51). Deutosternum has 8 teeth. Basal segment of chelicera 33μ, second segment 112μ, chela 40μ long.



50 51

FIGS. 50–51. *Steatonyssus* (*Steatonyssus*) *joaquimi* (Fonseca). Dorsal shields (fig. 50), venter and palptrochanter (fig. 51) of female.

Podonotal shield 276μ long, 240μ wide between setae *z*3, with eleven pairs of setae. Seta *i*2 extremely minute, about one-sixth the length of *i*3 ; seta *i*3 about two-thirds as long as *z*1 ; seta *i*5 about half as long as *z*3. Opisthonotal shield 300μ long, 180μ wide at level of setae *J*1, bearing 7 pairs of setae. Length of seta *J*2 about two-fifths the distance between *J*2 and *J*3 ; terminal setae not longer than the postero-laterals on the shield. Both shields appear to be reticulated, but the pattern is not distinct in the specimens examined.

Sternal shield reticulate, not demarcated anteriorly from the presternal area. Length from level of first pair of setae 42μ, width between second pair of setae 117μ. The posterior part of the shield is heavily sclerotized. First sternal seta about three-quarters as long as the second. Genital shield 126μ long from level of genital setae, 68μ wide between the setae ; length of setae about two-thirds the distance between their bases. Anal shield 96μ long to base of postanal seta, 75μ wide through middle of anus. Paranal setae level with posterior margin of anus and about three-fifths as long as the postanal seta.

The setae on the ventral part of the integument are about the same length as the genital setae, whereas those near the posterior margin and on the dorsum are longer (70μ) and stouter, tapering gradually. Peritreme extends to posterior fourth of coxa II, the peritrematal shield continuing to the anterior margin of coxa I. A small endopodal shield is present between coxae III and IV ; metapodal shields cannot be distinguished in these specimens.

Chaetotaxy of the legs typical for the genus. Length of tibia I, 96μ ; tarsus I, 165μ ; tibia IV, 87μ ; tarsus IV, 162μ ; basal width of tarsus IV, 36μ.

MALE. Described and figured by Fonseca (p. 92, figs. 3–4).

PROTONYMPH. Described and figured by Fonseca (p. 95, figs. 5–6).

HOSTS AND LOCALITIES. *Glossophaga soricina* (Pallas), Sao Paulo, Brazil (Fonseca, 1935). *Myotis albescens* (Geoffroy), Tacuaral, Paraguay, 12th November, 1900 [2 ♀♀ in the collection of the British Museum (Natural History)].

Steatonyssus (Steatonyssus) longipes Radovsky & Yunker

Steatonyssus longipes Radovsky & Yunker 1963, J. Parasit. **49** : 334, figs. 1–9.

FEMALE. Deutosternum has 8 teeth. Basal segment of chelicera 30μ, second segment 117μ, chelae about 45μ long.

Podonotal shield 264μ long, 198μ wide between setae *z*3, reticulate, bearing eleven pairs of setae. Length of seta *i*2 about half that of *i*3, and about half the distance between *i*4 and *z*2 ; seta *i*3 about two-thirds as long as *z*1 ; seta *i*5 slightly shorter than *z*3. Opisthonotal shield 336μ long, 156μ wide at the level of setae *J*1, bearing 7 pairs of setae. Setae *J*1–*J*3 relatively long and stout, length of *J*2 about three-fifths the distance between *J*2 and *J*3. Terminal setae slightly longer than the postero-laterals on the shield, about one-third the length of *J*2 ; subterminal setae minute. The ornamentation of the shield is not clearly visible in the specimen examined.

Anterior margin of sternal shield not sharply demarcated from the presternal area ; posterior part of shield has a granular appearance and a more compressed reticulate pattern than the anterior part. Length of shield from level of setae I is 54μ, width between setae II is 120μ. Sternal and metasternal setae subequal in length. Genital shield 126μ long from level of genital setae, 70μ wide between the setae ; length of genital setae slightly more than half the distance between their bases. The shield has a sharply pointed antero-median process extending over the sternal shield. The anal shield, which has an irregular anterior margin, is 123μ long to the base of the postanal seta, 87μ wide through the middle of the anus. Paranal setae level with the posterior margin of the anus, about the same length as the postanal seta.

Integument of idiosoma bears numerous setae. The ventral setae are slender and slightly longer than the genitals ; the postero-ventral and dorsal setae are stouter, the postero-dorsals having a maximum length of 54μ. Peritreme terminates behind anterior margin of coxa III ; peritrematal shield interrupted at level of posterior border of coxa II, the anterior leaf-like portion lying over coxae I and II. Very weakly sclerotized endopodal shields are visible between coxae III and IV ; metapodal shields cannot be distinguished with certainty.

Chaetotaxy of the legs typical for the genus (confirmed by Dr. F. Radovsky for six other specimens). Length of tibia I, 114μ ; tarsus I, 234μ ; tibia IV, 108μ ; tarsus IV, 234μ ; basal width of tarsus IV, 42μ.

MALE. Unknown.

PROTONYMPH. Podonotal shield 174μ long, 138μ wide between setae *z*3, bearing eleven pairs of setae. Pygidial shield 66μ long, 96μ wide, with 3 pairs of relatively long, stout, subequal setae and one pair of minute, subterminal microsetae. Anal shield 45μ long to base of postanal seta, 50μ wide through middle of anus.

Chaetotaxy of legs normal. Length of tibia I, 48μ ; tarsus I, 111μ ; tibia IV, 48μ ; tarsus IV, 111μ.

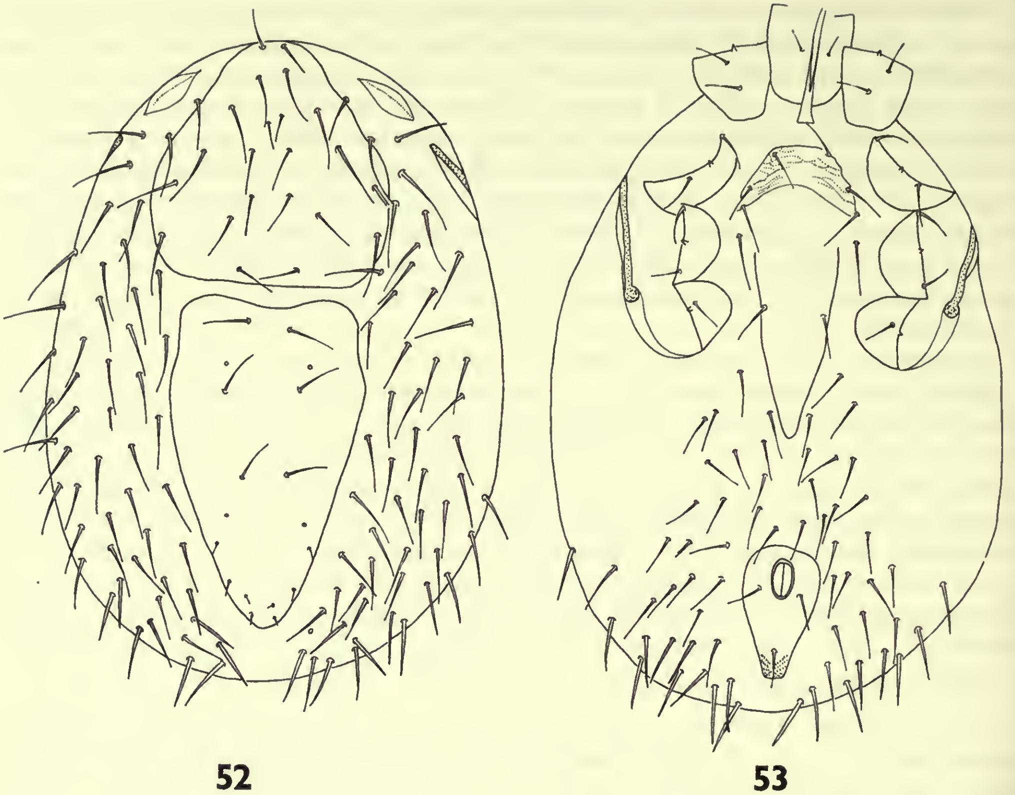
HOST AND LOCALITY. *Nycteris thebaica thebaica* Geoffroy, Abu Rawash, Imbaba, Giza, Egypt, collected by H. Hoogstraal, 9th February, 1960 (1 ♀ and 1 protonymphal paratype presented by Dr. F. Radovsky).

Steatonyssus (Steatonyssus) natalensis Zumpt & Patterson

Steatonyssus natalensis Zumpt & Patterson 1951, J. ent. Soc. S. Afr. **14** : 86, fig. 8.

FEMALE (Text-figs. 52–53). Deutosternum has 9 teeth. Basal segment of chelicera 30μ, second segment 96μ, chela 40μ long.

Podonotal shield 294μ long, 252μ wide between setae *z*3, bearing eleven pairs of setae. Length of setae *i*2 equal to the distance between *i*4 and *z*2, and about two-thirds the length of *i*3 ; seta *i*3 two-thirds as long as *z*1 ; seta *i*5 about three-fifths as long as *z*3. Opisthonotal shield 378μ long, 204μ wide at level of setae *J*1, bearing 7 pairs of setae. Setae *J*1–*J*3 relatively long, length of *J*2 half the distance between *J*2 and *J*3. The 4 pairs of posterior setae are very short, the terminals not longer than the postero-laterals. Both shields have a reticulate pattern.



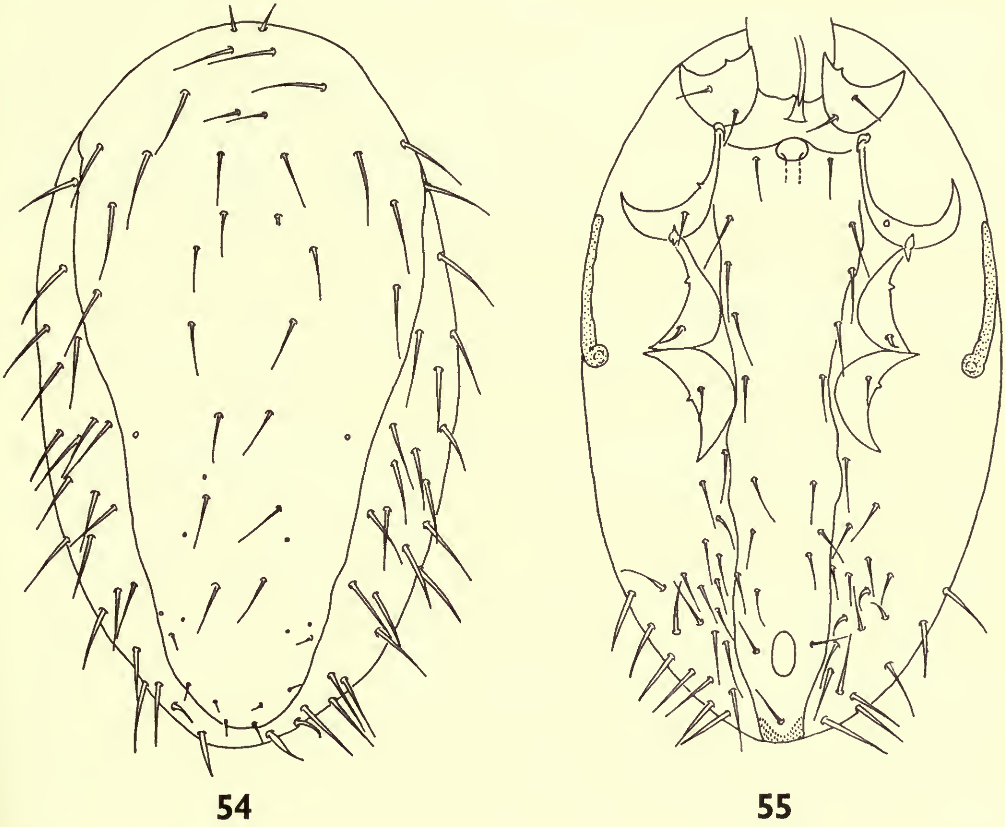
FIGS. 52–53. *Steatonyssus* (*Steatonyssus*) *natalensis* Zumpt & Patterson. Dorsum (fig. 52) and venter (fig. 53) of female.

Sternal shield about 40µ long, 114µ wide between second pair of setae. The specimen is over-cleared and flattened so that the boundaries and ornamentation of the shield are very indistinct. The posterior part of the shield does not appear to be thickened, but its reticulations, where visible, are more compressed than on the anterior part of the shield. Sternal setae subequal in length, the first pair very slightly shorter than the others. Genital shield 150µ long from level of genital setae, 70µ wide between the setae ; length of setae a little more than half the distance between their bases. Anal shield 124µ long to base of postanal seta, 90µ wide through middle of anus. Paranal setae antero-lateral to posterior margin of anus.

Integument of idiosoma bears numerous setae, including about 20 pairs of slender ventral setae which are about the same length as the genitals. Near the posterior margin of the body the setae are stout and blade-like, tapering rather abruptly at the extreme tip, and have a maximum length of about 63µ. On the remaining part of the dorsum the setae are about the same length as the posterior ones, but taper gently. Peritremes reach middle of coxa II ; peritrematal shields interrupted. Endo- and metapodal shields are not visible in this specimen.

Chaetotaxy of the legs typical for the genus. Length of tibia I, 96µ ; tarsus I, 156µ ; tibia IV, 96µ ; tarsus IV, 180µ ; basal width of tarsus IV, which is greatly flattened, is 50µ.

MALE (Text-figs. 54–55). Basal segment of chelicera 24µ, second segment 54µ, chela and spermadactyl 45µ. Dorsal shield 474µ long, 198µ wide between setae *z*3. It bears 12 pairs of setae on the anterior and 7 pairs on the posterior part.



FIGS. 54–55. *Steatonyssus* (*Steatonyssus*) *natalensis* Zumpt & Patterson. Dorsum (fig. 54) and venter (fig. 55) of male.

Holoventral shield bears 5 pairs of setae in the sternito-genital region and 4 pairs in the preanal region. The setae on the unsclerotized integument are less numerous than in the female, but similar in appearance. Peritremes barely extend beyond anterior margin of coxa III.

Chaetotaxy of legs as in female. Length of tibia I, 70µ ; tarsus I, 114µ ; leg IV is bent so that the segments can not be measured accurately ; length of tibia IV approximately 75µ ; tarsus IV approximately 130µ.

PROTONYMPH. Unknown.

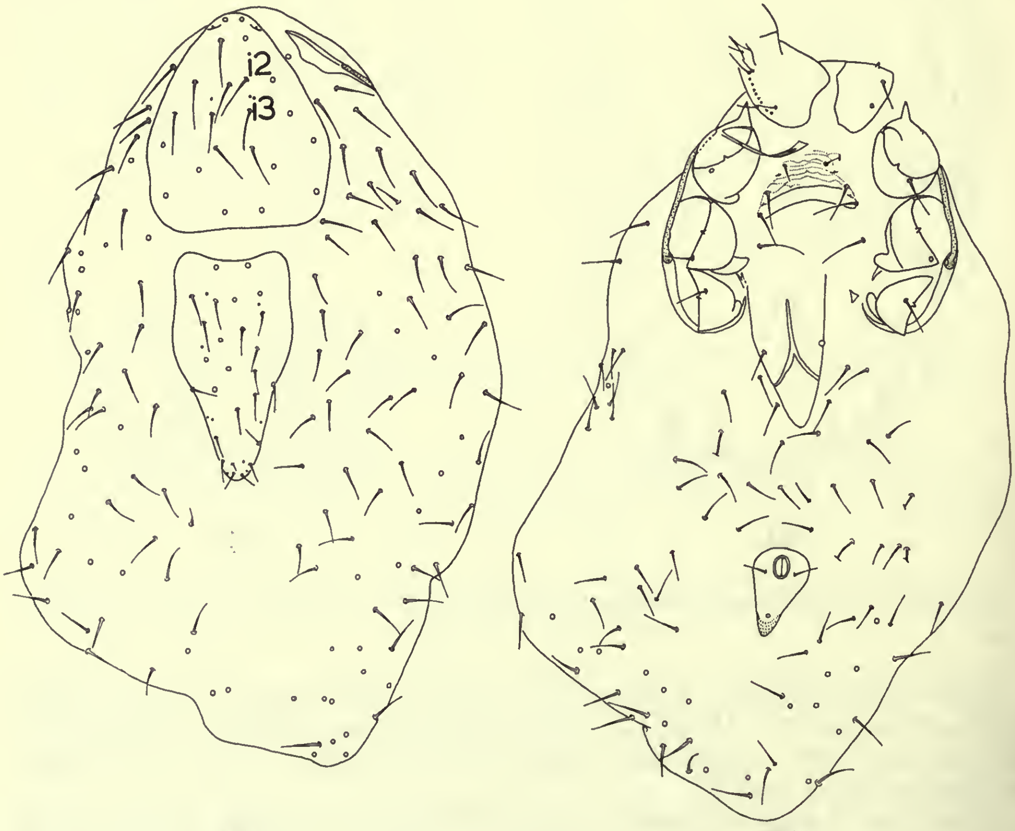
HOSTS AND LOCALITIES. *Miniopterus schreibersi natalensis* (Smith) from Pietermaritzburg, Natal, South Africa. (Holotype ♀ and paratype ♂ on loan from the South African Institute for Medical Research, Johannesburg.)

Steatonyssus (Steatonyssus) nyassae (Hirst)

Liponyssus nyassae Hirst 1922, Proc. zool. Soc. Lond. (1921) : 777.

FEMALE (Text-figs. 56–57). The gnathosoma is lying on its side so that details of its structure are not clearly visible.

Podonotal shield 264μ long, 186μ wide between setae *z*3, bearing eleven pairs of setae. Setae *i*2 and *i*3 subequal, nearly one and a half times the distance between *i*4 and *z*2 ; seta *i*3 about four-fifths the length of *z*1. Opisthonotal shield 276μ long, 140μ wide at the level of setae *J*1, bearing 27 setae. Terminal setae slightly shorter than the postero-laterals on the shield. Both shields have a reticulate pattern.



56 **57**

FIGS. 56–57. *Steatonyssus* (*Steatonyssus*) *nyassae* (Hirst). Dorsum (fig. 56) and venter (fig. 57) of female.

Sternal shield 63μ long, 99μ wide between setae II. The posterior portion of the shield forms a heavily sclerotized band. The length of the first pair of sternal setae cannot be determined as one seta is broken and the other is not lying flat. Genital shield 102μ long from level of genital setae, 72μ wide between the setae, with a pair of strongly marked lines which converge a little behind the genital setae. Anal shield 87μ long to base of postanal seta, 70μ wide through middle of anus. Paranal setae situated near posterior margin of anus.

Ventral setae of the integument about as long as the genital setae ; marginal setae stouter, the postero-dorsals having a maximum length of 45μ. Peritreme extends to middle of coxa II ; peritrematal shield continues anteriorly to middle of coxa I. A small endopodal shield is present between coxae III and IV ; metapodal shields cannot be distinguished in this specimen.

Chaetotaxy of the legs typical for the genus. Length of tibia I, 93μ ; tarsus I, 156μ ; tibia IV, 87μ ; tarsus IV cannot be measured.

MALE AND PROTONYMPH. Unknown.

HOST AND LOCALITY. " Elephant Shrew ", Chiromo, Nyasaland [type specimen in the collection of the British Museum (Natural History)]. *Scotophilus murinoflavus* (Heuglin), Torit, Sudan (Zumpt and Till, 1954).

Steatonyssus (Steatonyssus) occidentalis (Ewing)

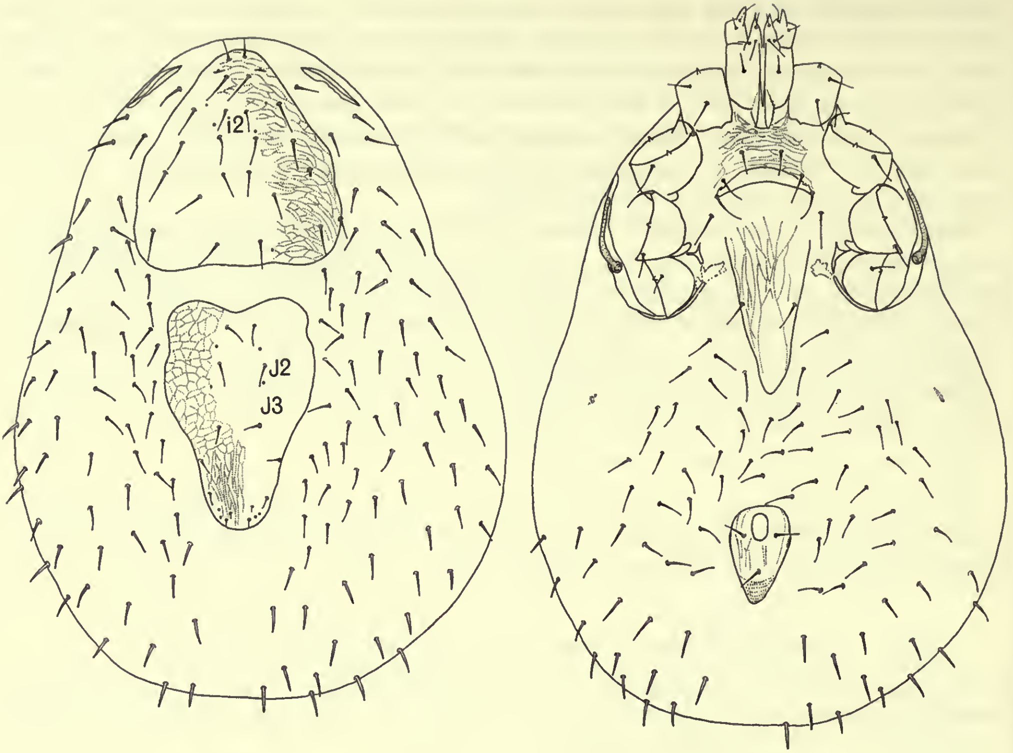
Ceratonyssus occidentalis Ewing 1933, Proc. U.S. nat. Mus. **82** (2971) : 10, pl. 3, fig. 5, pl. 4, fig. 1.
Steatonyssus occidentalis, Fonseca 1948, Proc. zool. Soc. Lond. **118** : 319 ; Radovsky & Furman 1963, Ann. ent. Soc. Amer. **56** : 272, figs.

FEMALE (Text-figs. 58–59). Deutosternal teeth not clearly visible. Basal segment of chelicera 24–27μ, second segment 82–99μ, chela 36μ long.

Podonotal shield reticulate, 252–276μ long, 210–222μ wide between setae *z*3. It bears eleven pairs of setae. Length of seta *i*2 about three-quarters that of *i*3 and slightly more than half the distance between *i*4 and *z*2 ; setae *i*3 and *i*5 almost as long as *z*1 and *z*3 respectively. Opisthonotal shield 270–288μ long, 168–180μ wide at the level of setae *J*1, with a reticulate pattern anteriorly and striations posteriorly. It bears 7 paris of setae, the terminals and subterminals being extremely small. Length of seta *J*2 is about one-third the distance between *J*2 and *J*3.

Sternal shield reticulate, anterior and lateral margins not very sharply defined, posterior portion heavily sclerotized. Length of shield 51–60μ, width between second pair of setae 102–110μ. Sternal and metasternal setae subequal in length. Genital shield 120–130μ long from level of genital setae, 66–68μ between the setae, with a pair of well marked, converging lines. Length of genital setae a little less than half the distance between their bases. Anal shield 78–84μ long to base of postanal seta, 72–78μ wide through middle of anus ; paranal setae near posterior margin of anus, about the same length as the postanal seta.

Integument of idiosoma bears numerous setae. The ventro-median ones are slender and about the same length as the genital setae. The postero-ventral and postero-dorsal setae are stouter and blade-like and have a maximum length of 30μ.



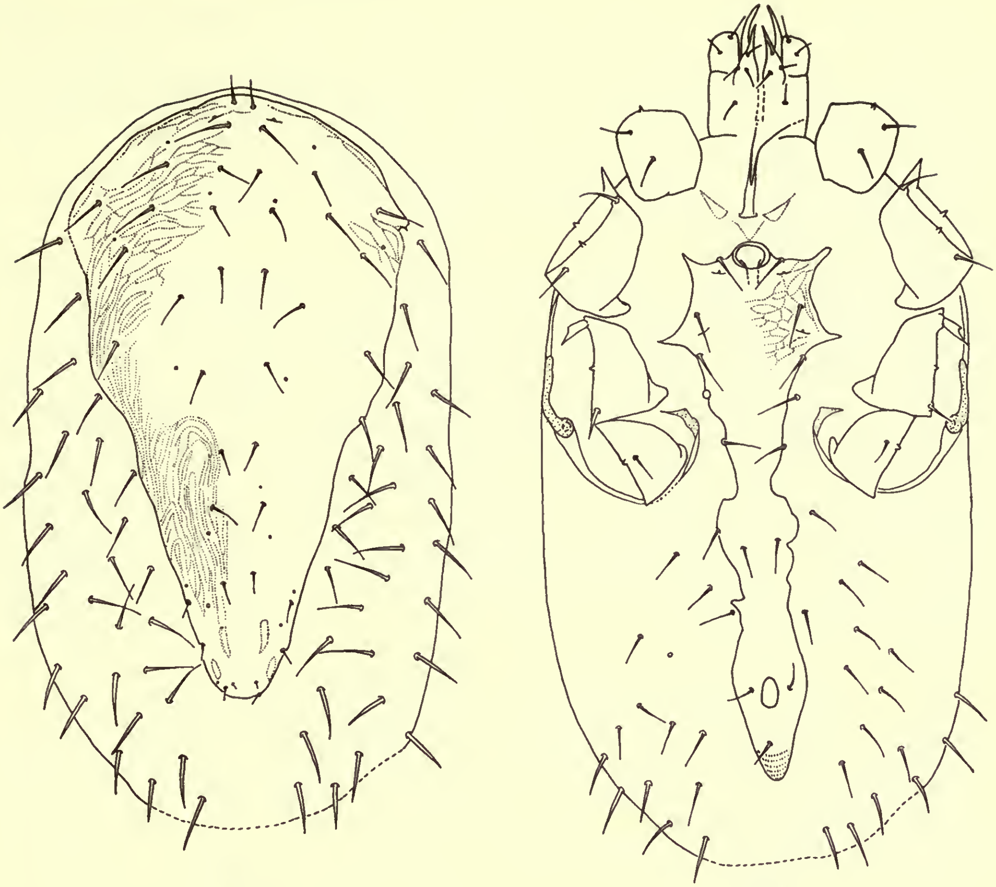
58 **59**

FIGS. 58–59. *Steatonyssus* (*Steatonyssus*) *occidentalis* (Ewing). Dorsum (fig. 58) and venter (fig. 59) of female.

The remaining dorsal setae are a little more slender, but are not as finely pointed as the ventro-median setae. Peritremes extend almost to anterior margin of coxa III ; peritrematal shields continue to posterior fourth of coxa II, where they are interrupted, the leaf-like anterior portion lying over the anterior half of coxa II and the posterior half of coxa I. A pair of endopodal shields is present between coxae III and IV, and a pair of very weakly sclerotized areas postero-lateral to coxae IV may represent the metapodal shields.

Chaetotaxy of the legs follows the typical *Steatonyssus* pattern. Length of tibia I, 66μ ; tarsus I, 117μ ; tibia IV, 60–69 ; tarsus IV, 120–129μ ; basal width of tarsus IV, 36μ.

MALE (Text-figs. 60–61). Basal segment of chelicera 27μ, second segment 66μ, chela and spermadactyl 40μ long. Dorsal shield 456μ long, 186μ wide between setae *z*3, bearing 19 pairs of setae and an additional marginal seta on one side. The anterior part of the shield, from about the level of seta *z*2, has a reticulate pattern. The remaining part of the shield has a pattern of striations which form whorls, rather like fingerprints, lateral to setae *J*1.



60 61

FIGS. 60–61. *Steatonyssus* (*Steatonyssus*) *occidentalis* (Ewing). Dorsum (fig. 60) and venter (fig. 61) of male.

Holoventral shield very narrow with irregular margins, bearing 15 setae. The shield is reticulate anteriorly, but from a little behind the metasternal setae there is a pattern of striations which continues on to the anterior part of the anal region. Paranal setae level approximately with middle of anus, about the same length as the postanal seta.

Unsclerotized integument of idiosoma bears about 45 pairs of setae of which 10–11 pairs are ventral in position and about the same length as the setae on the shield ; near the posterior margin and on the dorsum the setae are stouter and blade-like. Peritremes extend a little beyond the middle of coxa III, the peritrematal shields continuing to the posterior margin of coxa II.

Chaetotaxy of the legs as in the female. Coxa III has a broad, leaf-like, anterior seta. Length of tibia I, 54μ ; tarsus I, 87μ ; tibia IV, 57μ ; tarsus IV, 93μ.

PROTONYMPH. Podonotal shield 80μ long, 54μ wide between setae *z*3, with eleven pairs of setae. Pygidial shield with anterior, lateral and terminal setae, increasing in size in that order, and a pair of minute subterminals. The shield cannot be measured as the specimen is slightly damaged. Two pairs of mesonotal scutellae are present at the level of, and behind, setae *J*1. Anal shield 36μ long to base of postanal seta, 48μ wide through middle of anus.

Chaetotaxy of legs normal. Length of tibia I, 30μ ; tarsus I, 54μ ; tibia IV, 30μ ; tarsus IV, 54μ.

HOSTS AND LOCALITIES. *Eptesicus fuscus fuscus* (Palisot de Beauvois)?, North Fork, Madera Co., California, U.S.A., 28th July, 1950 (♂, ♀, protonymph presented by Dr. F. Radovsky). *Eptesicus fuscus pallidus* Young, North Fork, Madera Co., California, U.S.A., 14th July, 1950 (♀ presented by Dr. F. Radovsky). " Common Brown Bat," Adel, Oregon, U.S.A., 19th August, 1930 (cotype ♀ lent by United States National Museum). Radovsky and Furman (1963) record the following :— *Myotis velifer* (J. A. Allen), Los Lingos Canyon, Briscoe Co., Texas, U.S.A. *Corynorhinus* sp., Post, Garza Co., Texas, U.S.A. *Tadarida brasiliensis* (Geoffroy-Saint-Hilaire), Devil's Sink Hole, Edwards Co., Texas and Willcox, Cochise Co., Arizona, U.S.A. Yunker (1958) records this species from the following :— *Myotis lucifugus* (Le Conte), Maryland, U.S.A. *Lasiurus borealis* (Müller), Washington, D.C., U.S.A.

Steatonyssus (Steatonyssus) periblepharus Kolenati

Steatonyssus periblepharus Kolenati 1858, Wien. ent. Monatschr. **2** : 6 ; 1859, S.B. Akad. Wiss. Wien. **35** : 186, pl. 8, fig. 34 ; Oudemans 1936, Krit. Hist. Over. Acar. A (3) : 288 ; Willmann 1936, Zool. Anz. **114** : 153 ; Strandtmann & Wharton 1958, Manual of Mesostigmatid Mites : 113.

Steatonyssus brachypeltis Kolenati 1858, Wien. ent. Monatschr. **2** : 6 ; 1859, S. B. Akad. Wiss. Wien. **35** : 187, pl. 9, fig. 35.

Leiognathus arcuatus, Berlese 1889, Acar. Myr. Scorp. Italia fasc. 53 no. 8 (non *Dermanyssus arcuatus* Koch 1839).

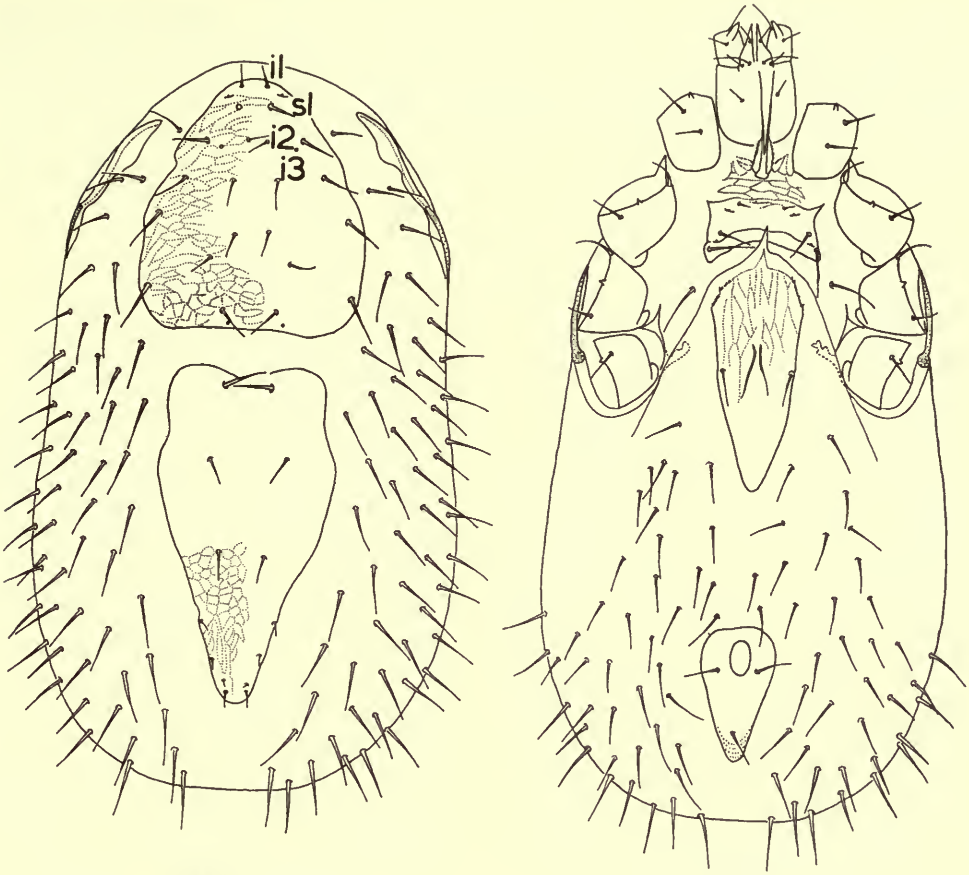
Liponyssus musculi, Oudemans 1902, Tijdschr. ned. Dierk. Ver. (2) **7** : 293, pl. 8, fig. 19–22, pl. 9, fig. 23–26 (nec *Acarus musculi* Schrank 1803, nec *Dermanyssus musculi* Koch 1836).

Liponyssus chiropteralis Hirst 1922, Proc. zool. Soc. Lond. (1921) : 776.

FEMALE (Text-figs. 62–63). Deutosternum has 8 teeth. Basal segment of chelicera 42μ, second segment 105μ, chelae 45–48μ long.

Podonotal shield 300–306μ long, 234–252μ wide between setae *z*3, bearing eleven pairs of setae. Setae *i*2 slightly shorter than *i*3, about three-quarters the distance between *i*4 and *z*2. Seta *i*3 half to two-thirds the length of *z*1 ; seta *i*5 half as long as *z*3. Opisthonotal shield 372–396μ long, 186–198μ wide at the level of setae *J*1, bearing 7 pairs of setae. Length of seta *J*2 about one-third the distance between *J*2 and *J*3 ; the 4 posterior pairs of setae are very short and fine. Both shields have a reticulate pattern.

Sternal shield not sharply demarcated from the reticulate presternal area ; concave posterior portion of shield heavily sclerotized. Length of shield 45–57μ, width between second pair of setae 114–126μ. Sternal seta I relatively short, not



62 **63**

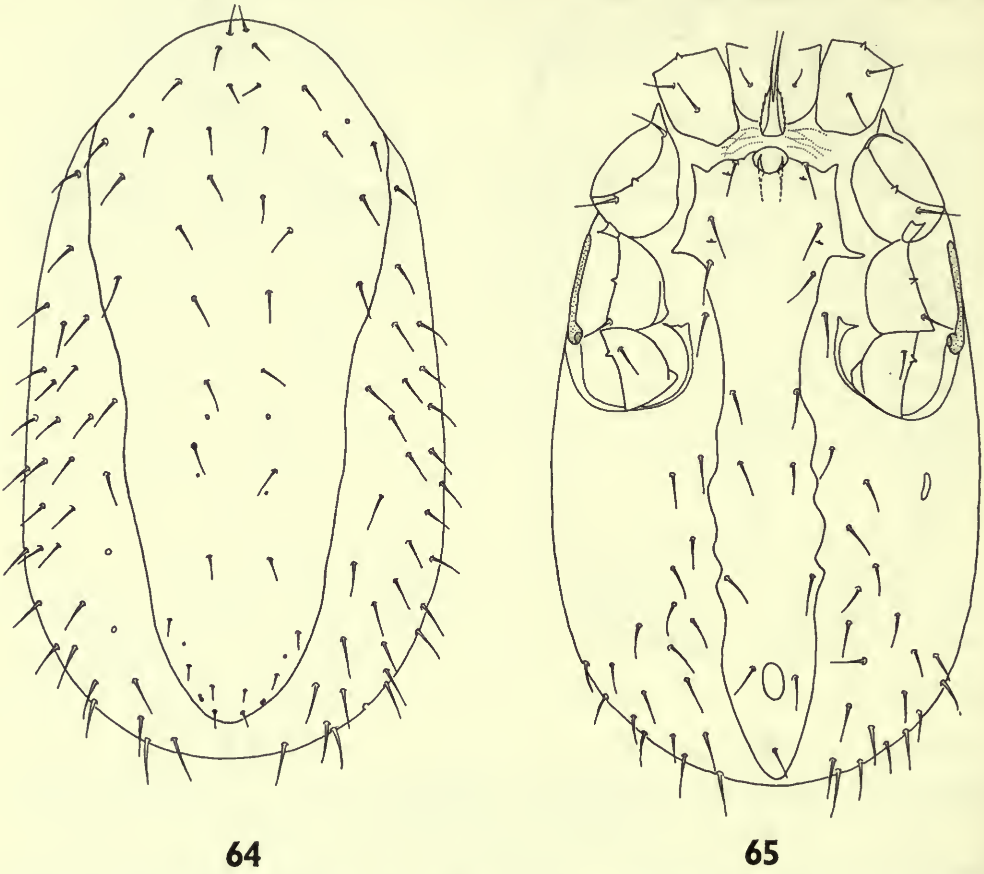
FIGS. 62–63. *Steatonyssus* (*Steatonyssus*) *periblepharus* Kolenati. Dorsum (fig. 62) and venter (fig. 63) of female.

more than half as long as seta II. Genital shield 144–156μ long from level of genital setae, 78–87μ wide between the setae ; length of genital setae little more than half the distance between their bases. Anal shield pear-shaped, 126–135μ long to base of postanal seta, 84–94μ wide through middle of anus. Paranal setae level with posterior third of anus, approximately as long as the postanal seta.

Integument of idiosoma bears numerous setae, the dorsal and marginal ones being longer (65μ) and stouter than the ventral ones. Peritremes reach middle of coxa II, the peritrematal shields continuing to the middle of coxa I. Endopodal shields present between coxae III and IV ; metapodal shields not visible.

Chaetotaxy of the legs follows the typical *Steatonyssus* pattern. Coxa II bears a large antero-dorsal spine which usually appears pointed, but in certain positions it can be seen to terminate in 4 small denticles. Length of tibia I, 96–102μ ; tarsus I, 156–162μ ; tibia IV, 90–102μ ; tarsus IV, 174–192μ ; basal width of tarsus IV, 42μ.

MALE (Text-figs. 64–65). Basal cheliceral segment 30μ, second segment 66μ, chela and spermadactyl 60μ long. Dorsal shield 552–564μ long, 186–192μ wide between setae *z*3, bearing 12 pairs of setae on the anterior half and 7 pairs on the posterior part. It has an overall reticulate pattern.



FIGS. 64–65. *Steatonyssus* (*Steatonyssus*) *periblepharus* Kolenati. Dorsum (fig. 64) and venter (fig. 65) of male.

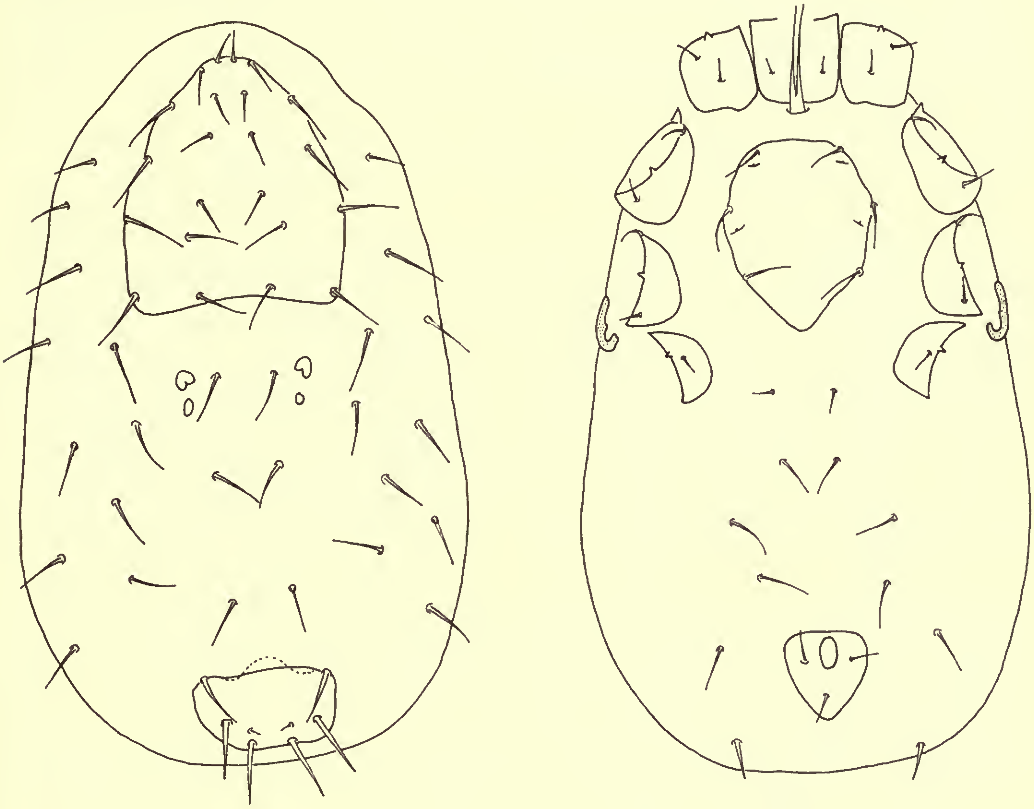
Holoventral shield bears 4 pairs of setae in the sternito-genital region, the metasternals being situated on the integument beside the shield. From 4 to 8 setae are present in the preanal region. Integument of the idiosoma bears 50–52 pairs of setae which are longer and stouter towards the caudal end of the body. Peritremes extend to the anterior margin of coxa III.

Chaetotaxy of legs as in the female. Anterior seta on coxa III very broad with two terminal processes, one rather flat and the other slightly longer and pointed. Length of tibia I, 75–78μ ; tarsus I, 132μ ; tibia IV, 72μ ; tarsus IV, 126μ.

PROTONYMPH (Text-figs. 66–67). Basal segment of chelicera 15μ, second segment

60μ, chela 27μ long. Podonotal shield 160μ long, 132μ wide between setae *z*3, bearing eleven pairs of setae. Pygidial shield 66μ long, 93μ wide, with 4 pairs of setae, 3 relatively long, stout, pairs and a pair of very short subterminal setae. Two pairs of small mesonotal scutellae are present at the level of setae *J*1. Anal shield triangular, 48μ long to base of postanal seta, 54μ wide through middle of anus.

Chaetotaxy of legs normal. Length of tibia I, 45μ ; tarsus I, 84μ ; tibia IV, 42μ ; tarsus IV, 84μ.



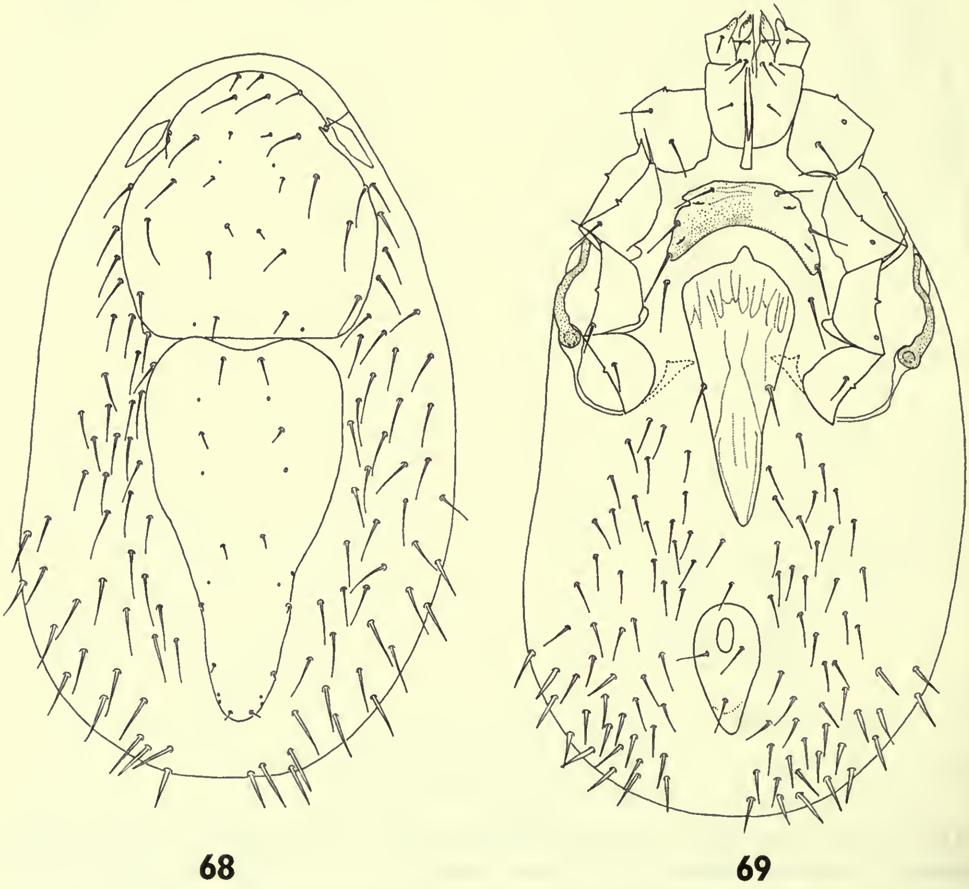
FIGS. 66–67. *Steatonyssus* (*Steatonyssus*) *periblepharus* Kolenati. Dorsum (fig. 66) and venter (fig. 67) of protonymph.

HOSTS AND LOCALITIES. The following material in the collection of the British Museum (Natural History) has been examined:— *Pipistrellus kuhli* (Kuhl), Algeria. *Pipistrellus pipistrellus* (Schreber), Stoke Poges, Buckinghamshire, 15th August, 1956 ; Colchester, Essex, December, 1961–January, 1962 (coll. G. B. Thompson) ; Coles Hill, Co. Fermanagh, N. Ireland, 14th October, 1960 (coll. S. Skillen) ; Enniskillen, Co. Fermanagh, N. Ireland, May–June, 1962 (coll. R. Palmer). *Myotis mystacinus* (Kuhl), Easington, Yorkshire, 1st September, 1931 (coll. T. Warwick) ; Styal, Cheshire, 30th April, 1932 (coll. C. Jones). " Bats " from Ain Sefra, S.W. Algeria.

The following additional hosts and localities have been recorded in the literature :— *Pipistrellus pipistrellus* (Schreber), Germany ; *Myotis capaccinii* (Bonaparte), Hungary and Germany ; *Myotis emarginatus* (Geoffroy), Germany (Kolenati, 1859). *Eptesicus serotinus* (Schreber), Germany (Oudemans, 1902).

Steatonyssus (Steatonyssus) radovskyi sp. nov.

FEMALE (Text-figs. 68–69). Deutosternum appears to have 9 or 10 teeth, but these are not very distinct in the specimens examined. Basal segment of chelicera 27μ, second segment 87μ, chelae 36μ long.



FIGS. 68–69. *Steatonyssus* (*Steatonyssus*) *radovskyi* sp. nov. Dorsum (fig. 68) and venter (fig. 69) of female.

Podonotal shield 282μ long, 222μ wide between setae *z*3. It bears 13 pairs of setae, one pair being on the extreme margin of the shield ; one specimen has an additional marginal seta on one side. Setae *i*2 minute, three-fifths as long as *i*3 and less than one-third the distance between *i*4 and *z*2 ; seta *i*3 about one-third the length of *z*1 ; seta *i*5 less than half as long as *z*3. Opisthonotal shield 354–375μ long, 180–198μ wide at level of setae *J*1. It bears 6 pairs of setae of which *J*1 is the longest ; length of seta *J*2 less than one-fifth the distance between *J*2 and *J*3. The postero-lateral and terminal setae are minute ; the subterminals are absent. Both shields are reticulate. Sternal shield 45μ long, 135–140μ wide between second pair of setae ; it has a granular appearance with a few faint reticulations, and the posterior region is only slightly denser than the anterior region. Sternal and metasternal setae subequal, the first pair being very slightly shorter than the others. Genital shield 135–144μ long from level of genital setae, 68–75μ wide between the setae; length of genital setae about three-quarters the distance between their bases. Anal shield 99–102μ long to base of postanal seta, 70–75μ wide through middle of anus. Paranal setae level with posterior margin of anus, about the same length as the postanal seta.

Integument of idiosoma bears about 94 pairs of setae ; the ventral ones are slender and hair-like, the dorsal ones are slightly longer and the posterior ones are thick and spine-like. The postero-dorsal setae have a maximum length of 48μ, the caudals are relatively shorter and stouter, measuring 40μ. Peritremes short, scarcely extending beyond the anterior margin of coxa III ; peritrematal shields interrupted, the anterior leaf-like portion lying over the anterior part of coxa II and the posterior margin of coxa I. Endopodal and metapodal shields are not distinguishable in the specimens examined.

Chaetotaxy of the legs typical for the genus. Length of tibia I, 66–69μ ; tarsus I, 130–135μ ; tibia IV, 70–75μ ; tarsus IV, 156–165μ ; basal width of tarsus IV, 48μ.

MALE AND PROTONYMPH. Unknown.

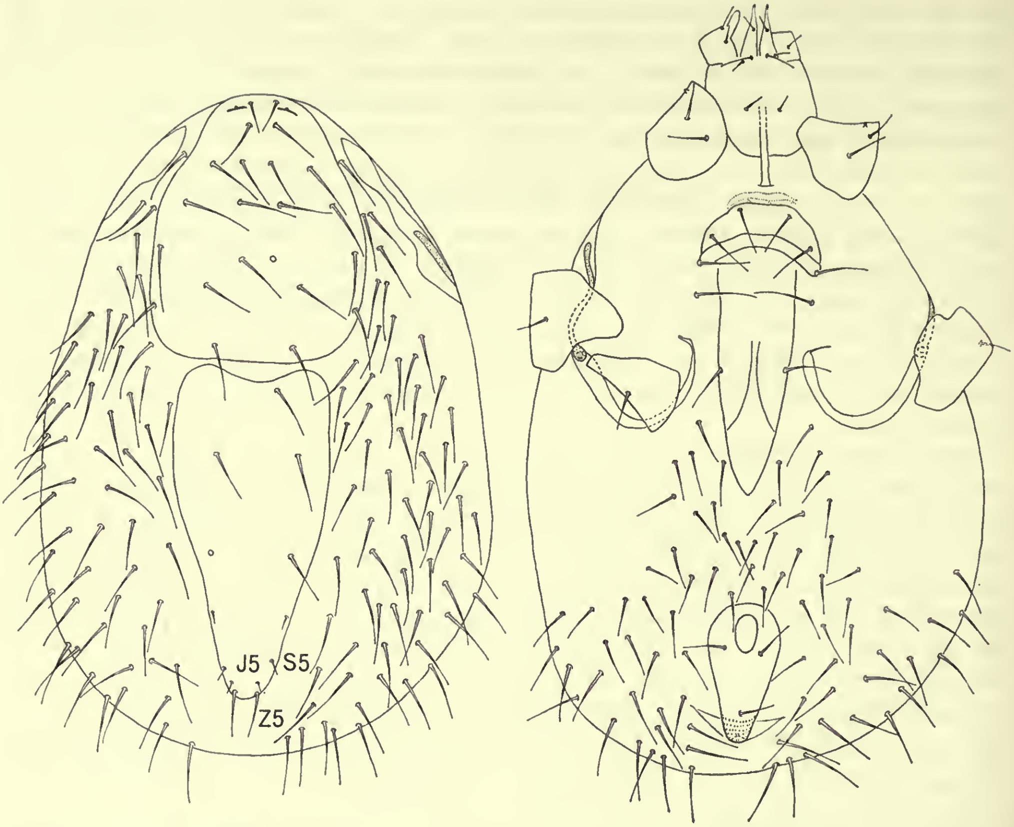
HOST AND LOCALITIES. *Dasypterus intermedius* (H. Allen), 6 females collected by R. B. Eads, Military Highway, Cameron Co., U.S.A., 27th February, 1962 (presented by Capt. V. J. Tipton). One female collected by J. Wiseman, San Antonio, Texas, U.S.A., 4th October, 1962 (presented by Dr. F. Radovsky). Holotype (1963.11.11.34), 4 ♀ paratypes (1963.11.11.35–38) in the collection of the British Museum (Natural History) ; 1 ♀ paratype presented to Dr. F. Radovsky ; 1 ♀ paratype deposited in the United States National Museum, Washington, D.C.

Steatonyssus (Steatonyssus) spinosus Willmann

Steatonyssus spinosus Willmann 1936, Zool. Anz. **114** : 152, figs. 1–5.

FEMALE (Text-figs. 70–71). The number of deutosternal teeth cannot be determined. Basal segment of chelicera 40μ, second segment 120μ, chela about 48μ long.

Podonotal shield 295μ long, 220μ wide between setae *z*3, bearing eleven pairs of setae. Length of setae *i*2 approximately equal to the distance between *i*4 and *z*2, and about four-fifths the length of *i*3 ; seta *i*3 about five-sixths as long as *z*1 ; seta *i*5 slightly shorter than *z*3. Opisthonotal shield 342μ long, 168μ wide at the level of seta *J*1, with 7 pairs of setae (one member of the first pair is absent in the specimen examined). Length of seta *J*2 slightly more than half the distance between



70 **71**

FIGS. 70–71. *Steatonyssus* (*Steatonyssus*) *spinosus* Willmann. Dorsum (fig. 70) and venter (fig. 71) of female.

*J*2 and *J*3 ; terminal setae about 45µ long, two and a half times as long as the postero-lateral setae on the shield. Both shields have a reticulate pattern.

Sternal shield about 48µ long, 114µ wide between second pair of setae ; anterior and lateral margins rather indistinct, posterior portion heavily sclerotized. Sternal and metasternal setae subequal in length. Genital shield 138µ long from level of genital setae, 75µ wide between the setae ; length of genital setae nearly as long as the distance between their bases. Anal shield elongate, pear-shaped, 123µ long to base of postanal seta, 80µ wide through middle of anus. Paranal setae level with posterior margin of anus, slightly longer than postanal seta.

Integument of idiosoma bears numerous setae, the dorsal and posterior setae being coarser than the ventrals ; the postero-dorsal setae have a maximum length of 72µ. Peritreme extends a short distance beyond the anterior margin of coxa III ; peritrematal shield continues to the middle of coxa I. Endopodal shields are present between coxae III and IV, and a pair of weakly sclerotized metapodal shields is visible behind coxae IV.

Chaetotaxy of the legs typical for the genus. Length of tibia I, 96µ ; tarsus I, 180µ ; tibia IV, 96µ ; tarsus IV, 192µ ; basal width of tarsus IV, which is somewhat flattened, is 54µ.

MALE AND PROTONYMPH. Unknown.

HOST AND LOCALITY. *Solenodon paradoxus* Brandt, Hamburg Zoological Institute, December, 1935 [1 ♀ in the collection of the British Museum (Natural History)]. *Vespertilio superans* Thomas, Voroshilov, U.S.S.R., 7th July, 1946 (1♀ amongst some specimens of *S. superans* sent by Dr. N. G. Bregetova).

Steatonyssus (Steatonyssus) sudanensis (Hirst)

Liponyssus sudanensis Hirst 1926, Proc. zool. Soc. Lond. **3** : 835.

FEMALE (Text-figs. 72–73). Deutosternum has 9 teeth. Basal segment of chelicera 27µ, second segment 135µ, chelae 36µ long.

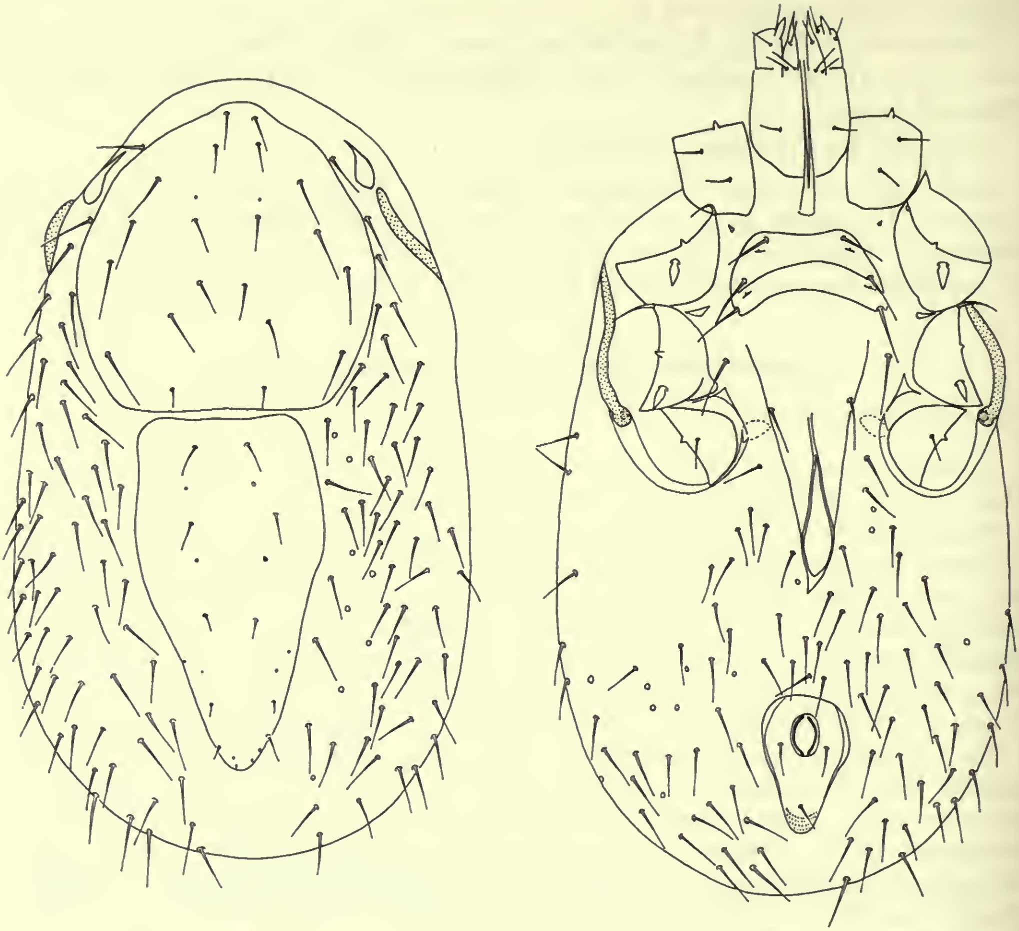
Podonotal shield 288–294µ long, 222–228µ wide between setae *z*3, bearing 10 pairs of setae. Setae *i*2 are absent ; lengths of setae *i*3 and *i*5 about two-thirds the lengths of *z*1 and *z*3 respectively. Opisthonotal shield 315–336µ long, 150–160µ wide at the level of setae *J*1, bearing 5 pairs of setae. Length of seta *J*2 about one-third the distance between *J*2 and *J*3. The terminal and subterminal setae are absent. The two pairs of postero-lateral setae are short and fine except in one specimen, which has a longer seta on one side only. Both shields have a reticulate pattern.

Sternal shield clearly demarcated from reticulate presternal area ; posterior portion heavily sclerotized. Length of shield 54µ, width between second pair of setae 111–120µ. Sternal seta I about five-sixths as long as seta II. Genital shield terminates in an extremely fine point and its posterior surface bears two strongly sclerotized linear markings which converge near the middle of the shield. Length of shield, from level of genital setae, is 192µ ; width between bases of setae is 66µ ; length of genital setae nearly equal to the distance between their bases. Anal shield pear-shaped, 102–108µ long to base of postanal seta, 76–84µ wide through middle of anus. Paranal setae near posterior margin of anus, slightly longer than the postanal seta.

Integument of idiosoma bears numerous dorsal and ventral setae, the longest of the postero-dorsal setae measuring about 48µ. Peritreme extends to anterior fourth of coxa II ; peritrematal shield interrupted, the anterior part extending to the middle of coxa I. Endopodal shields are present between coxae III and IV, and very small ones between coxae I and II, and between coxae II and III. Metapodal shields are not clearly visible.

The chaetotaxy of the legs differs from the typical *Steatonyssus* pattern in that tibia I lacks seta pd_3. The posterior setae on coxae II and III are stout and spine-like. The segments of the first pair of legs are not suitable for measurement ; length of tibia IV is 84µ and of tarsus IV is 192µ ; basal width of tarsus IV is 40µ.

MALE AND PROTONYMPH. Unknown.



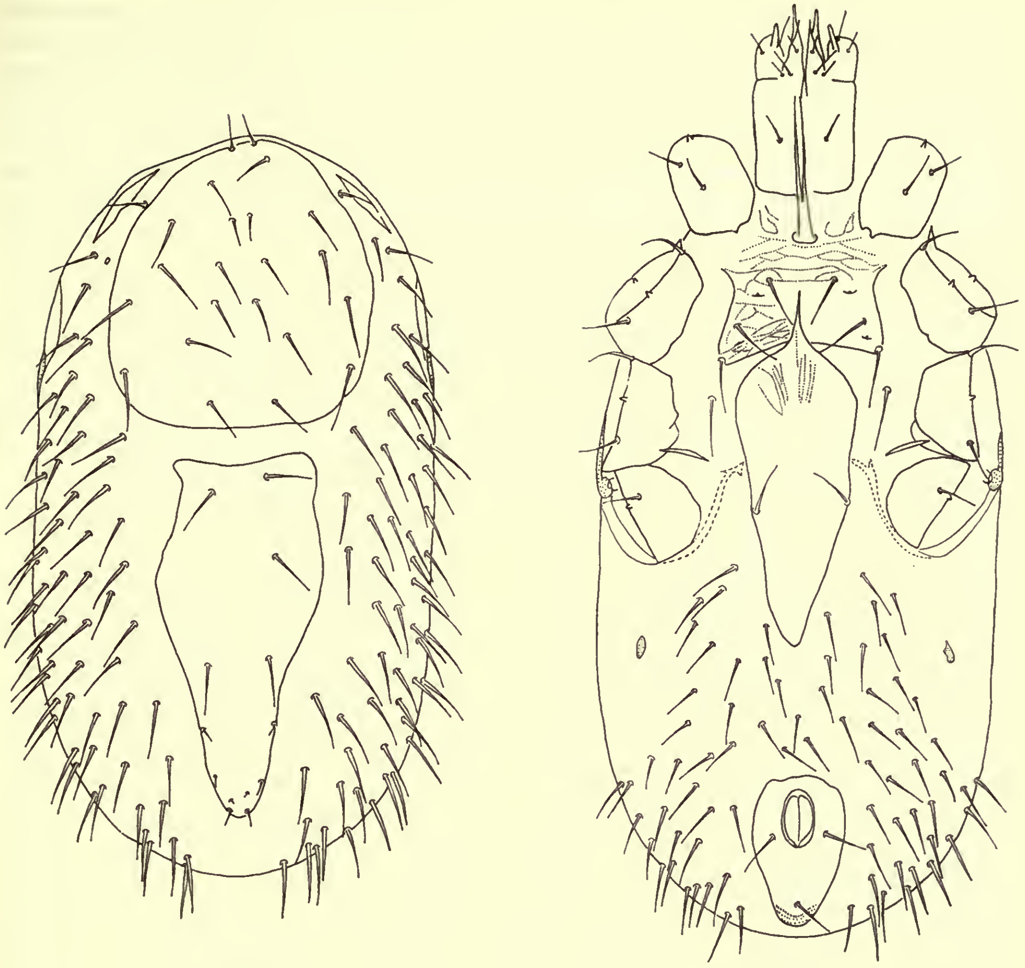
FIGS. 72–73. *Steatonyssus* (*Steatonyssus*) *sudanensis* (Hirst). Dorsum (fig. 72) and venter (fig. 73) of female.

HOST AND LOCALITY. *Taphozous nudiventris* (Cretzschmar) from Khartoum, Sudan, 9th December, 1925 [female paratypes in the collection of the British Museum (Natural History)].

Steatonyssus (Steatonyssus) tibialis sp. nov.

FEMALE (Text-figs. 74–75). Deutosternum has 8 teeth. Basal segment of chelicera 30μ, second segment 114μ, chelae about 40μ long.

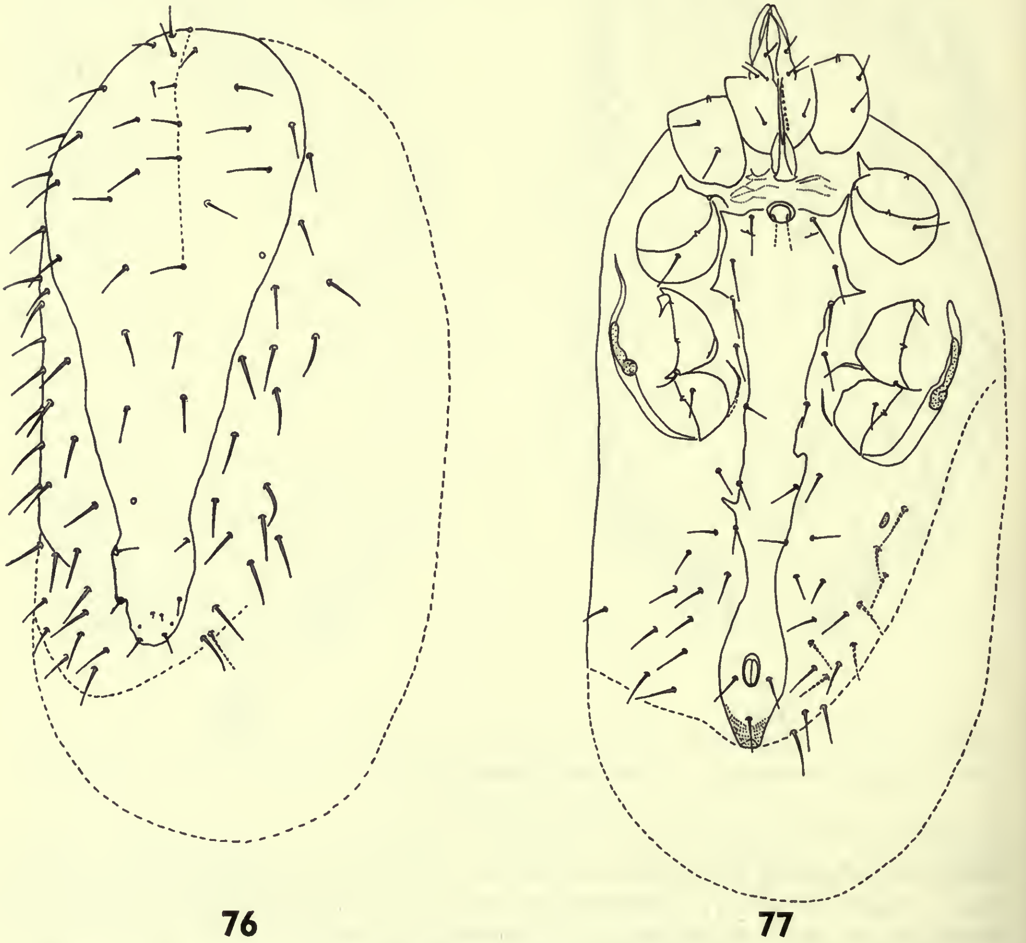
Podonotal shield 258–276μ long, 204–222μ wide between setae *z*3, bearing eleven pairs of setae. Length of seta *i*2 slightly more than half that of *i*3 ; setae *i*3 and *i*5 approximately two-thirds as long as setae *z*1 and *z*3 respectively. Opisthonotal



FIGS. 74–75. *Steatonyssus* (*Steatonyssus*) *tibialis* sp. nov. Dorsum (fig. 74) and venter (fig. 75) of female.

shield 318–348μ long, 132–156μ wide at level of setae *J*1, bearing usually 7 pairs of setae. Length of seta *J*2 about half the distance between *J*2 and *J*3. Seta *J*2 is missing on one side in the holotype, *J*1 is missing on one side in one of the paratypes ; a third paratype has an additional unpaired seta at the level of *J*3. The terminal and postero-lateral setae on the shield are subequal in length and do not exceed one-third the length of seta *J*2. Both shields are weakly reticulate.

Anterior margin of sternal shield not demarcated from reticulate presternal area ; posterior border a little more heavily sclerotized than rest of shield, with a slight granulation and with a more compressed reticulate pattern. Length of shield from level of first pair of setae is 54–60μ, width between second pair of setae is 114–120μ. Sternal and metasternal setae subequal in length. Genital shield 126–150μ long from level of genital setae, 84μ wide between the setae ; length of genital setae about half the distance between their bases. The shield has a sharply pointed antero-median process which extends over the sternal shield. The anal shield, which has an irregular anterior margin, is 108–120μ long to the base of the postanal seta, 84–90μ wide through the middle of the anus. The paranal setae are on a level between the middle and posterior margin of the anus.



FIGS. 76–77. *Steatonyssus* (*Steatonyssus*) *tibialis* sp. nov. Dorsum (fig. 76) and venter (fig. 77) of male.

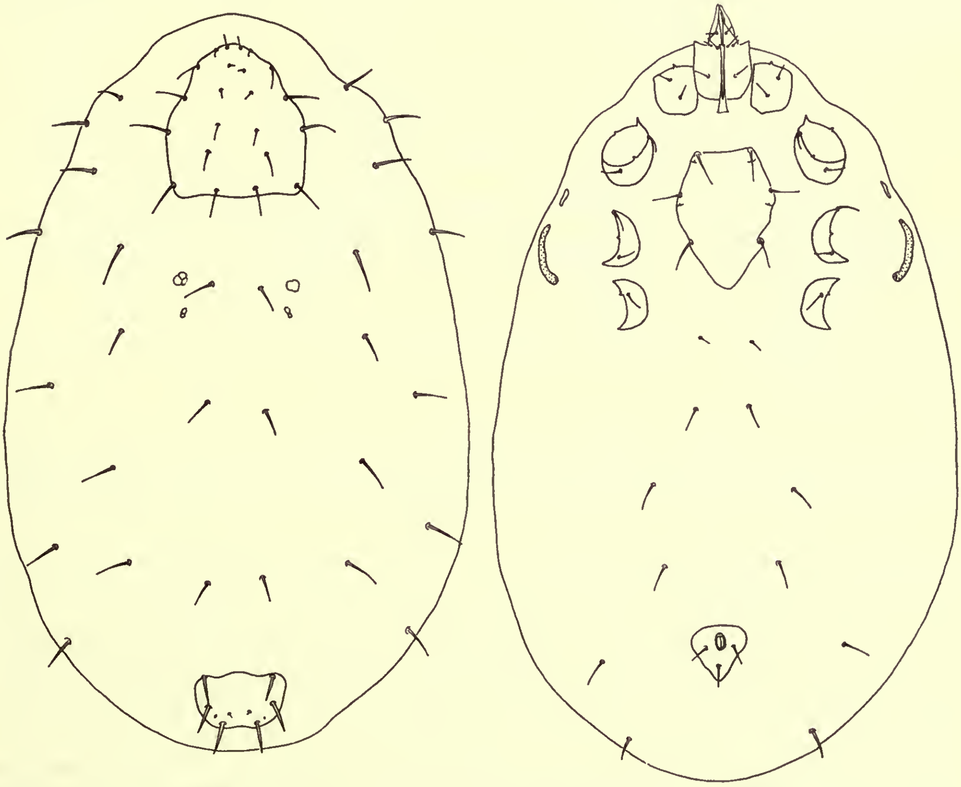
Integument of idiosoma bears 96–97 pairs of setae. The ventral setae are slender and about the same length as the genitals ; the dorsal setae are slightly longer and stouter, those near the posterior margin having a maximum length of 48μ.

Peritremes terminate at a point level approximately with the middle of coxa III ; peritrematal shield interrupted at posterior margin of coxa II, the separated leaf-like portion lying over the anterior part of coxa II and the posterior margin of coxa I. A pair of slender endopodal shields is situated between coxae III and IV, and a pair of very weakly sclerotized, roughly oval, metapodal shields behind coxae IV.

The chaetotaxy of the legs differs from the typical *Steatonyssus* pattern in that tibiae III and IV each have an additional dorsal seta, ad_2. Length of tibia I, 102μ ; tarsus I, 228μ ; tibia IV, 117μ ; tarsus IV, 234μ ; basal width of tarsus IV, 40μ.

MALE (Text-figs. 76–77). Only one damaged specimen is available in which the chelae are retracted ; the deutosternum has 8 teeth. Dorsal shield 510μ long, 168μ wide between setae *z*3. Chaetotaxy similar to that of the female except that seta *J*3 is missing on one side.

Holoventral shield very narrow with irregular lateral margins. It bears 3 pairs of setae in the sternal region, one pair of genitals, and 2 pairs of setae in the preanal



78 **79**

FIGS. 78–79. *Steatonyssus* (*Steatonyssus*) *tibialis* sp. nov. Dorsum (fig. 78) and venter (fig. 79) of protonymph.

region. The metasternals are situated on the striated integument beside the shield. Peritremes short, as in the female.

Chaetotaxy of legs as in the female. Anterior seta on coxa III has a broad, almost rectangular, basal portion, extended into a lateral point. Length of tibia I 75µ ; tarsus I, 150µ ; tibia IV, 78µ ; tarsus IV, 153µ.

PROTONYMPH (Text-figs. 78–79). Podonotal shield 190µ long, 150µ wide between setae *z*3, bearing eleven pairs of setae. Pygidial shield 75µ long, 105µ wide, with 3 pairs of relatively long, stout setae and one pair of minute subterminal setae. Anal shield 48µ long to base of postanal seta, 66µ wide through middle of anus. Chaetotaxy of legs normal. Length of tibia I, 51µ ; tarsus I, 111µ ; tibia IV, 51µ ; tarsus IV, 117µ.

HOST AND LOCALITY. *Nycteris thebaica capensis* Smith, Kanye, Bechuanaland Protectorate, collected by Dr. F. Zumpt, 9th December, 1957. Holotype, 3 ♀ paratypes, 2 protonymphs in the collection of the South African Institute for Medical Research, Johannesburg ; allotype ♂ (1963.11.11.45), 4 ♀ paratypes (1963.11.11.46–49) and 3 protonymphs (1963.11.11.50–52) in the collection of the British Museum (Natural History).

Subgenus ***STEATONYSSELLA*** nov.

Type : *Steatonyssus furmani* Tipton & Boese, 1958

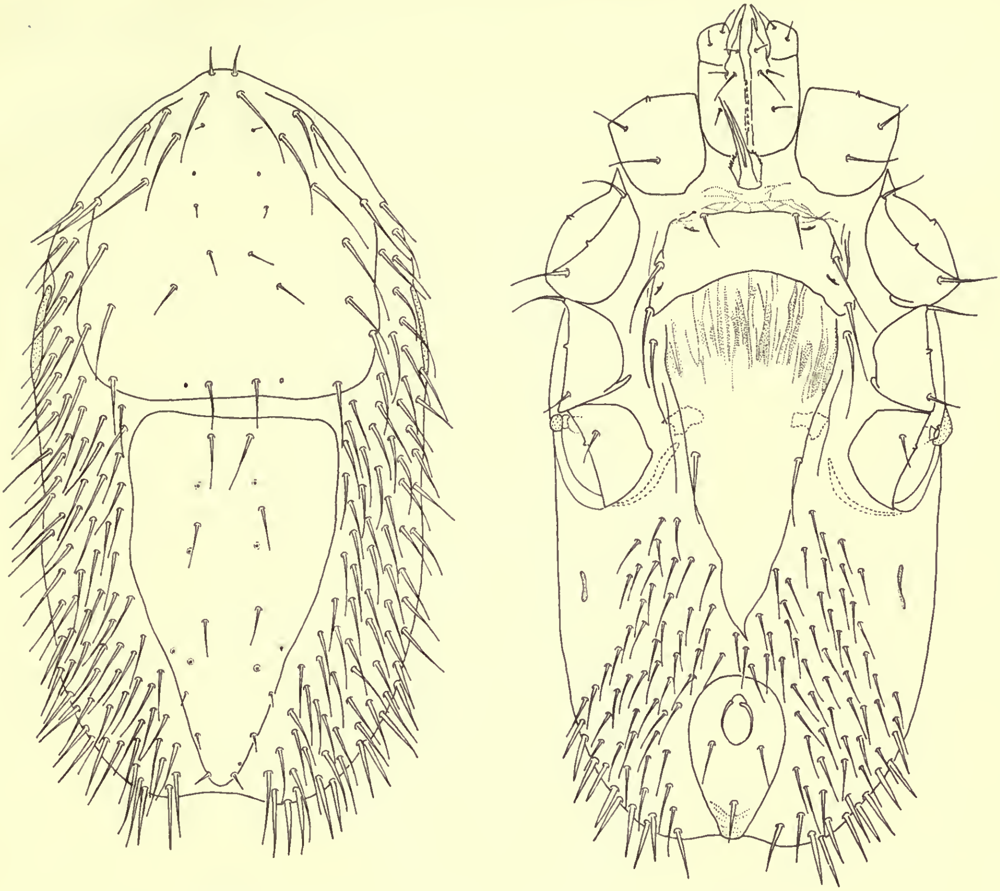
Steatonyssus (Steatonyssella) furmani Tipton & Boese

Steatonyssus furmani Tipton & Boese 1958, Proc. ent. Soc. Wash. **60** : 80, figs. 1–4 ; Radovsky & Furman 1963, Ann. ent. Soc. Amer. **56** : 274.

FEMALE (Text-figs. 80–81). Deutosternal teeth not clearly visible. First cheliceral segment 21µ, second segment 66µ, chela 34µ long. Palp without a trochantal process.

Podonotal shield 249–252µ long, 170–180µ wide between setae *z*3, bearing 16 pairs of setae. Setae *i*2 minute, about two-thirds the length of *i*3 and not more than one-sixth the distance between *i*4 and *z*2. Seta *i*3 about one-seventh the length of *z*1 ; seta *i*5 approximately two-thirds as long as *z*3. Opisthonotal shield 282–288µ long, 150µ wide at level of setae *J*1 ; it bears 6 pairs of setae, the subterminals being absent. Length of setae *J*2 less than half the distance between *J*2 and *J*3 ; the three posterior pairs of setae are very short, the terminals (12µ) not more than twice as long as the longest postero-laterals. The three pairs of submedian and one pair of postero-lateral pores have thickened rims. The anterior shield is reticulate, but the ornamentation of the posterior shield is not distinct in the specimens examined.

Sternal shield 45–48µ long, 135–145µ wide between the second pair of setae ; it is weakly sclerotized, without ornamentation, and is clearly demarcated anteriorly from the reticulate presternal area. Sternal seta I not quite half the length of setae II ; setae II–IV subequal in length. Genital shield 126–138µ long from level of genital setae, terminating in a sharp point ; 70–78µ wide between the setae ;



80 81

FIGS. 80–81. *Steatonyssus* (*Steatonyssella*) *furmani* Tipton & Boese. Dorsum (fig. 80) and venter (fig. 81) of female.

length of genital setae about two-thirds the distance between their bases. Anal shield 96–108μ long to base of postanal seta, 69–72μ wide through middle of anus ; paranal setae level with posterior margin of anus.

Integument of idiosoma bears numerous setae. Ventral setae three-quarters as long as the genitals, becoming stout and spine-like near the posterior margin. Dorsal setae about as long as the genitals, stouter near the margin of the body ; postero-dorsal setae have a maximum length of 54μ. Peritremes extend almost to anterior margin of coxa III ; peritrematal shield interrupted at level of posterior margin of coxa II, the separated leaf-like portion extending from anterior fourth of coxa II to posterior margin of coxa I. Endopodal shields cannot be distinguished ; weakly sclerotized, elongate metapodal shields are present behind coxae IV.

Chaetotaxy of the legs follows the typical *Steatonyssus* pattern. Length of tibia I, 60μ ; tarsus I, 105μ ; tibia IV, 66μ ; tarsus IV, 140μ ; basal width of tarsus IV, 42μ.

MALE (Text-fig. 82). Deutosternal teeth not clearly visible. First cheliceral segment 21μ, second segment 57μ, chela and spermadactyl 42μ long.

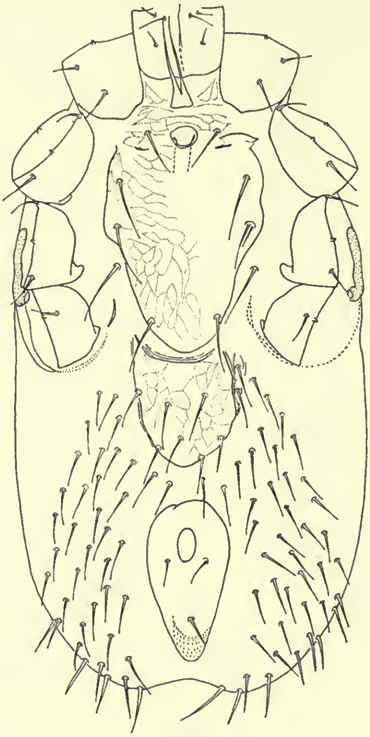


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FIG. 82. *Steatonyssus* (*Steatonyssella*) *furmani* Tipton & Boese. Venter of male.

Form and chaetotaxy of dorsal shields as in the female. Podonotal shield 198μ long, 156μ wide between setae *z*3. Opisthonotal shield 235μ long, 110μ wide at level of setae *J*1. The venter bears three separate shields. Sternito-genital shield reticulate, not clearly demarcated from the presternal area, bearing 3 pairs of sternal setae and one pair of genitals ; metasternal setae situated on the striated integment beside the shield. Ventral shield also reticulate, concave anteriorly, bearing 7 setae. Anal shield similar to that of female, 87μ long to base of postanal seta, 60μ wide through middle of anus.

Setae on integument of idiosoma similar in form to those of the female, but less numerous. Peritremes as in female ; metapodal shields not clearly distinguishable.

Chaetotaxy of legs as in female. Length of tibia I, 45μ ; tarsus I, 75μ ; tibia IV, 48μ ; tarsus IV is bent and cannot be measured.

PROTONYMPH. Described by Radovsky & Furman (p. 274).

HOST AND LOCALITIES. *Lasiurus borealis* (Müller), Yolo Co., California, U.S.A., collected by D. Constantine, 10th–12th August, 1954 (1 ♂, 2 ♀♀ lent by Dr. F. Radovsky). Recorded from the same host in Indiana (Tipton & Boese, 1958) and in Illinois and New York (Radovsky & Furman, 1963).

Species Incertae Sedis

We have been unable to examine the type material of the following seven species which have been referred to the genus *Steatonyssus*.

1. *Steatonyssus abramus* Wang Dwen-Ching, 1963.
   Acta Ent. Sinica **12** (1) : 57, figs. 7–8.
2. *Dermanyssus avium* Wagner, 1841.
   Icon. Zool. t. 25, f.11.
3. *Steatonyssus hubli* Hiregaudar & Bal, 1956.
   Current Sci. **24** : 221 (1955), (*nom. nud.*).
   Agra Univ. J. Res. (*Sci.*) **5** : 107, figs.
4. *Steatonyssus longispinosus* Wang Dwen-Ching, 1963.
   Acta Ent. Sinica **12** (1) : 58, figs. 9–10.
5. *Dermanyssus murinus* Lucas, 1840.
   Hist. nat. Crust. Arachn. Myr. : 479.
6. *Steatonyssus superans* Zemskaya, 1951.[1]
   Avtoref. Dissert. Mosk. Gos. Univ., Moskva : 1–11 ;
   Bregetova, 1956. *Akad. Sci. U.S.S.R.* **61** : 162.
7. *Dermanyssus vespertilionis* Dugès, 1834.
   Ann. Sci. nat. (2), **1** : 18.

HOST-PARASITE LIST

CHIROPTERA

Antrozous pallidus pacificus Merriam
Steatonyssus (*Steatonyssus*) *antrozoi* Radovsky & Furman

Coleura afra (Peters)
Steatonyssus (*Steatonyssus*) *calcaratus* Radovsky & Yunker

Corynorhinus spec.
Steatonyssus (*Steatonyssus*) *occidentalis* (Ewing)

Cynopterus sphinx (Vahl)
Steatonyssus (*Steatonyssus*) *evansi* Delfinado
Steatonyssus (*Steatonyssus*) *faini* Delfinado

---

[1] Since completing this paper we have received specimens of *Steatonyssus superans* Zemskaya, by courtesy of Dr. N. G. Bregetova. In our key, this species comes out with *Steatonyssus* (*S.*) *occidentalis* (Ewing), from which it can be distinguished as follows : The peritreme is longer, extending approximately to the middle of coxa II. At the posterior end of the body there are about eight pairs of thick, stiff, rod-like setae which taper abruptly at the tips.

Dasypterus intermedius (H. Allen)
Steatonyssus (*Steatonyssus*) *radovskyi* sp. nov.

Eidolon helvum (Kerr)
Steatonyssus (*Steatonyssus*) *javensis brevisetosus* ssp. nov.

Eptesicus fuscus fuscus (Palisot de Beauvois)
Steatonyssus (*Steatonyssus*) *antrozoi* Radovsky & Furman
Steatonyssus (*Steatonyssus*) *occidentalis* (Ewing)

Eptesicus fuscus pallidus Young
Steatonyssus (*Steatonyssus*) *occidentalis* (Ewing)

Eptesicus serotinus (Schreber)
Steatonyssus (*Steatonyssus*) *periblepharus* Kolenati

Eptesicus tenuipinnis (Peters)
Steatonyssus (*Steatonyssus*) *javensis brevisetosus* ssp. nov.

Glossophaga soricina (Pallas)
Steatonyssus (*Steatonyssus*) *joaquimi* (Fonseca)

Hipposideros cyclops (Temminck)
Steatonyssus (*Steatonyssus*) *hipposideros* Till

Lasiurus borealis (Müller)
Steatonyssus (*Steatonyssus*) *occidentalis* (Ewing)
Steatonyssus (*Steatonyssella*) *furmani* Tipton & Boese

Miniopterus schreibersi natalensis (Smith)
Steatonyssus (*Steatonyssus*) *natalensis* Zumpt & Patterson

Myotis spec.
Steatonyssus (*Steatonyssus*) *emarginatus* Radovsky & Furman

Myotis albescens (Geoffroy)
Steatonyssus (*Steatonyssus*) *joaquimi* (Fonseca)

Myotis bocagei (Peters)
Steatonyssus (*Steatonyssus*) *javensis brevisetosus* ssp. nov.

Myotis capaccinii (Bonaparte)
Steatonyssus (*Steatonyssus*) *periblepharus* Kolenati

Myotis emarginatus (Geoffroy)
Steatonyssus (*Steatonyssus*) *periblepharus* Kolenati

Myotis lucifugus (Le Conte)
Steatonyssus (*Steatonyssus*) *occidentalis* (Ewing)

Myotis mystacinus (Kuhl)
Steatonyssus (*Steatonyssus*) *periblepharus* Kolenati

Myotis velifer (J. A. Allen)
Steatonyssus (*Steatonyssus*) *occidentalis* (Ewing)

Myotis yumanensis (H. Allen)
Steatonyssus (*Steatonyssus*) *emarginatus* Radovsky & Furman

Nycteris spec.
Steatonyssus (*Steatonyssus*) *brucei* Lavoipierre

Nycteris macrotis Dobson
Steatonyssus (*Steatonyssus*) *afer* Radovsky & Yunker

Nycteris thebaica capensis Smith
Steatonyssus (*Steatonyssus*) *tibialis* sp. nov.

Nycteris thebaica thebaica Geoffroy
Steatonyssus (*Steatonyssus*) *longipes* Radovsky & Yunker

Nycticeius humeralis (Rafinesque)
Steatonyssus (*Steatonyssus*) *ceratognathus* (Ewing)

Pipistrellus abramus (Temminck)
Steatonyssus (*Steatonyssus*) *abramus* Wang Dwen-Ching
Steatonyssus (*Steatonyssus*) *longispinosus* Wang Dwen-Ching

Pipistrellus babu Thomas
Steatonyssus (*Steatonyssus*) *javensis javensis* Oudemans

Pipistrellus ceylonicus (Kelaart)
Steatonyssus (*Steatonyssus*) *hubli* Hiregaudar & Bal

Pipistrellus hesperus (H. Allen)
Steatonyssus (*Steatonyssus*) *emarginatus* Radovsky & Furman

Pipistrellus kuhli (Kuhl)
Steatonyssus (*Steatonyssus*) *periblepharus* Kolenati

Pipistrellus nanus (Peters)
Steatonyssus (*Steatonyssus*) *afer* Radovsky & Yunker
Steatonyssus (*Steatonyssus*) *brucei* Lavoipierre
Steatonyssus (*Steatonyssus*) *eos* Zumpt & Till

Pipistrellus pipistrellus (Schreber)
Steatonyssus (*Steatonyssus*) *periblepharus* Kolenati

Rhinolophus foxi Thomas
Steatonyssus (*Steatonyssus*) *aelleni* Radovsky & Yunker

Rhinolophus landeri lobatus Peters
Steatonyssus (*Steatonyssus*) *benoiti* sp. nov.

Scotophilus kuhli Leach*
Steatonyssus (*Steatonyssus*) *evansi* Delfinado
Steatonyssus (*Steatonyssus*) *faini* Delfinado

Scotophilus murinoflavus (Heuglin)
[*? = Scotophilus leucogaster* (Cretzschmar)]
Steatonyssus (*Steatonyssus*) *nyassae* (Hirst)

Scotophilus nigrita (Schreber)
Steatonyssus (*Steatonyssus*) *brucei* Lavoipierre

Scotophilus temminckii (Horsfield)
Steatonyssus (*Steatonyssus*) *evansi* Delfinado
Steatonyssus (*Steatonyssus*) *faini* Delfinado

Tadarida brasiliensis (Geoffroy-Saint-Hilaire)
Steatonyssus (*Steatonyssus*) *occidentalis* (Ewing)

Tadarida spillmanni Monard
Steatonyssus (*Steatonyssus*) *crassisetosus* sp. nov.

Taphozous nudiventris (Cretzschmar)
Steatonyssus (*Steatonyssus*) *sudanensis* (Hirst)

Triaenops afer Peters
Steatonyssus (*Steatonyssus*) *calcaratus* Radovsky & Yunker

Vespertilio superans Thomas
Steatonyssus (*Steatonyssus*) *spinosus* (Willmann)
Steatonyssus (*Steatonyssus*) *superans* Zemskaya

Unidentified Bats
Steatonyssus (*Steatonyssus*) *afer* Radovsky & Yunker
Steatonyssus (*Steatonyssus*) *ceratognathus* (Ewing)
Steatonyssus (*Steatonyssus*) *evansi* Delfinado
Steatonyssus (*Steatonyssus*) *faini* Delfinado
Steatonyssus (*Steatonyssus*) *javensis javensis* (Oudemans)
Steatonyssus (*Steatonyssus*) *occidentalis* (Ewing)

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* Considered by J. R. Ellerman and T. C. S. Morrison-Scott (*Checklist of Palaearctic and Indian Mammals.* London. 1951) as not specifically identifiable. This record may refer either to *Scotophilus heathi* (Horsfield) or to *Scotophilus temminckii* (Horsfield).

INSECTIVORA

Solenodon paradoxus Brandt
Steatonyssus (*Steatonyssus*) *spinosus* Willman

" Elephant Shrew "
Steatonyssus (*Steatonyssus*) *nyassae* (Hirst)

SUMMARY

1. The external morphology and classification of the genus *Steatonyssus* (Laelaptidae : Macronyssinae) are reviewed. The genus is divided into two subgenera : *Steatonyssus* s. str. (type *Steatonyssus periblepharus* Kol.) and *Steatonyssella* subgen. nov. (type *Steatonyssus furmani* Tipton & Boese).

2. Twenty-six species and subspecies are recognized of which the following five are considered new to science :

S. (*Steatonyssus*) *benoiti* sp. nov.
S. (*Steatonyssus*) *crassisetosus* sp. nov.
S. (*Steatonyssus*) *javensis brevisetosus* ssp. nov.
S. (*Steatonyssus*) *radovskyi* sp. nov.
S. (*Steatonyssus*) *tibialis* sp. nov.

3. *Steatonyssus primus* Grokhovskaya & Nguen-Huan-Hoe and *Steatonyssus secundus* Grokhovskaya & Nguen-Huan-Hoe are considered to be synonymous with *Steatonyssus evansi* Delfinado and *Steatonyssus faini* Delfinado, respectively.

4. A key is given for the identification of females of the genus and a host-parasite list is included.

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FORM AND FUNCTION IN THE EVOLUTION OF THE VERMETIDAE

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25 MAY 1965
NATURAL HISTORY

J. E. MORTON

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ZOOLOGY Vol. 11 No. 9
LONDON: 1965

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BY

J. E. MORTON
Department of Zoology,
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Pp. 583–630 ; 15 *Text-figures* ; 1 *Diagram*

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FORM AND FUNCTION IN THE EVOLUTION OF THE VERMETIDAE

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1. INTRODUCTION

An awareness of the living animal is always important to the evolutionary morphologist : it is nowhere more so than in the mesogastropod family Vermetidae, which have lost all external traces of snail form and produce loosely coiled worm tubes welded to or embedded in the substrate. In a literal sense vermetids are tied to their environment and their adaptations to this new mode of life are peculiarly intimate and far-reaching. The study of structure as reflecting function was for long neglected in the Vermetidae. The pioneering papers are those of Boettger (1930) on mucous feeding in *Serpulorbis gigas*, and Yonge (1932) on ciliary feeding in an Australian species. They were followed by Yonge and Iles (1939), a brief description in MacGinitie & MacGinitie (1949), and Morton (1951a ; 1955).

Yet a study of adaptive morphology, however rewarding, is not in itself sufficient for an understanding of evolutionary history. Adaptive features are unreliable as guides to natural arrangement and the classifier must look for conservative characters unlikely to be too much influenced by evolutionary convergence, which becomes more frequent and confusing as the mode of life becomes more specialised. The conchologist must usually have the last word in taxonomy at the generic level, not only because shell characters are the most accessible to study in collections, but chiefly because the features in which he is interested are more likely to be immune from convergence due to similar modes of life. Till the present time vermetid taxonomy has proceeded upon the evidence of the shell, usually in the absence of the apex and of the operculum. Compilers of faunas and check-lists have approached this family with a distaste evoked by no other, and have hastily left it after a decent minimum of provisional re-arrangement.

Dr. Myra Keen's paper (1961) has now given us the first firmly grounded generic classification of Vermetidae, on the basis of the coiling pattern, apex and operculum throughout the family. For the first time it is possible to consider the impact of adaptation to mode of life in validly drawn generic groups. At intervals from 1949 onwards I have had the advantage of correspondence and later of personal discussions with Dr. Keen. She has generously proveded me with preserved animals and kept me in constant touch with the progress of her taxonomic studies. From investigation of the Vermetidae from our different points of view has now emerged a broad-based agreement in our ideas upon evolution and generic relationships.

The progress in vermetid classification during the last 30 years will be apparent on comparing Thiele's (1929) arrangement of the family with that possible today. Of two genera conservatively adopted by him, one, *Tenagodus* (*Siliquaria*), has become the basis of another family with only a convergent resemblance to true Vermetidae. Into the Siliquariidae has passed also one of six subgeneric groups of Thiele's *Vermetus* s.l. (each more usually regarded as a genus)—namely *Stephopoma* ; while a second of these six, *Vermicularia*, belongs close to the Siliquariidae, preferably in a separate family, Vermiculariidae. These two families show close affinities with Turritellidae.

Dr. Keen has recognised five genera in the family Vermetidae as now restricted, namely *Vermetus*, *Serpulorbis*, *Petaloconchus*, *Dendropoma* and the new genus *Tripsycha*. The last is monotypic, and gives recognition to the peculiar mode of coiling, in a closely wound hollow cone, of *Vermetus tripsycha* Pilsbry and Lowe, 1932, a form evidently closely allied to *Petaloconchus*. The four large groups have been adequately studied malacologically, and can be seen to make up a homogeneous and workable family, with a series of well-marked evolutionary trends.

The Vermetidae have no clear annectant features with any other group known at present. There is no reason to break up their loose association with the other families of Thiele's large and loosely defined Stirps Cerithiacea.

It is too early yet to give a definite account of vermetid functional morphology or evolution. My object here is to bring together what we at present know of the malacological features of each genus of Vermetidae, and of their adaptive peculiarities and possible evolution. In addition to living material of *Dendropoma* (*Novastoa*) *lamellosum*, *Serpulorbis aotearoicus* and *S. zelandicus*, I have examined preserved material of representative species, including several examples of each genus. For a few species, my material was crudely preserved, and in the crucial species *V. adansonii* was resuscitated after drying! Here it was a matter of being grateful for what facts I could cull ; I have at least learned from experience to get the best from such specimens as I had. I shall not deal exhaustively with the anatomy of any one species here : it is hardly useful to attempt this in the absence of observations from life. With each genus I have attempted to give representative figures showing the

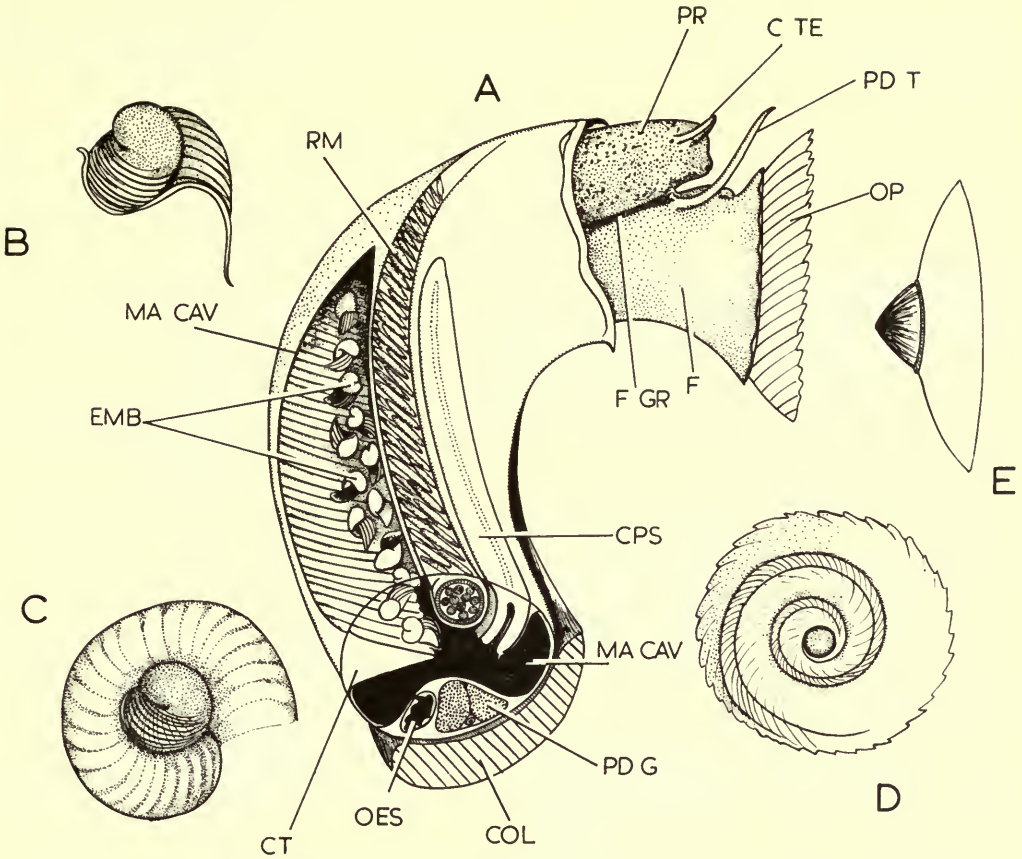

FIG. 1. *Dendropoma marchadi.* A. The anterior part of the animal illustrated diagrammatically, with the incision of the mantle to show its contents. B. The apex at the beginning of post-embryonic growth. C. The apex showing the embryonic shell encircled by the first post-embryonic whorl, shown from beneath after detaching from the substrate. D. Operculum in upper view. E. Operculum in side view.

nature and location of the structures chiefly involved in the differentiation of the group, especially in the cephalic, pedal and pallial regions. The figures of the animal, operculum and nuclear whorls of *Dendropoma marchadi* show pretty well the key characters that are important in any examination of new vermetid material. Reference to the diagrammatic sagittal sections of *Dendropoma maximum*, (Text-fig. 2C), *D.* (*Novastoa*) *lamellosa* (Text-fig. 3G) and *Serpulorbis squamigerus* (Text-fig. 9A) will also be helpful in illustrating the range of structure and adaptations of the soft parts shown within the family.

It is unlikely that I shall have an early opportunity to work again with living vermetids ; and this paper will have achieved its purpose if it makes clear that Dr. Keen's four generic groups stand out equally naturally upon the evidence of the animal as on conchological features. I offer my present findings as a starting point for a student on some shore more favoured by these reticent but charming gastropods.

2. GENERIC REVIEW

(i) Genus ***DENDROPOMA*** Mörch, 1861

Species examined :

1. *D.* (*Dendropoma*) *leucozonias* (Mörch, 1861) ; West Africa. B.M. (N.H.) Reg. No. 195926.
2. *D.* (*Dendropoma*) *lituella* (Mörch, 1861) ; California.
3. *D.* (*Dendropoma*) *maximum* (Sowerby, 1825) ; Queensland, Australia. B.M. (N.H.) Reg. No. 1856.9.24.45. B.M. (N.H.) Reg. No. 1870.13.23.21. B.M. (N.H.) Reg. No. 1952.1.29.290.
4. *D.* (*Dendropoma*) *rastrum* (Mörch, 1861) ; California. B.M. (N.H.) Reg. No. 195916.
5. *D.* (*Dendropoma*) *marchadi* Keen & Morton, 1960 ; East Africa.
6. *D.* (*Novastoa*) *lamellosum* (Hutton, 1873) ; New Zealand.
7. *D.* (*Novastoa*) *irregulare* (Orbigny, 1842) ; Jamaica.
8. *D.* (*Novastoa*) *corallinaceum* (Tomlin, 1939) ; South Africa. B.M. (N.H.) Reg. No. 1953.3.12.93–94.
9. *D.* (*Novastoa*) *ghanaense* Keen & Morton, 1960 ; Ghana.
10. *D.* (*Novastoa*) *tholia* Keen & Morton, 1960 ; Mozambique.
11. *" Dendropoma B " :* Undescribed sp. from South Africa (see Keen & Morton, 1960).

Keen (1961) has clearly set out the diagnostic features of this genus, including the brown-coloured, one to two-whorled inflated nucleus, characteristic modes of coiling and sculpture, and the prevalence of the corroding habit. The operculum, though showing a wide range of variation in shape and proportions, is always greater in diameter than the foot and has a distinctive character in the axial mamilla which constitutes its centre and is only occasionally wanting.

The operculum is the most obvious and accessible classificatory character provided by the *Dendropoma* animal, and the species of this genus could be arranged upon opercular characters in three groups, not necessarily however coinciding with their natural descent or with subdivisions upon other anatomical grounds. First there are those species with the operculum upwardly concave, forming a thin and sharp-edged saucer or bowl, either with the axial mamilla very prominent as in *D. lamellosum*, much reduced as in *D. lituella* and *D. marchadi*, or almost or entirely lacking as in *D. leucozonias* and *D. maximum*. Secondly, the operculum may be flat or only very slightly concave, with the mamilla small or lacking and the insertion surface strengthened by a polished annular thickening, as in *D. corallinaceum* and *D. rastrum*. The third group of species, typified by *D. tholia*,

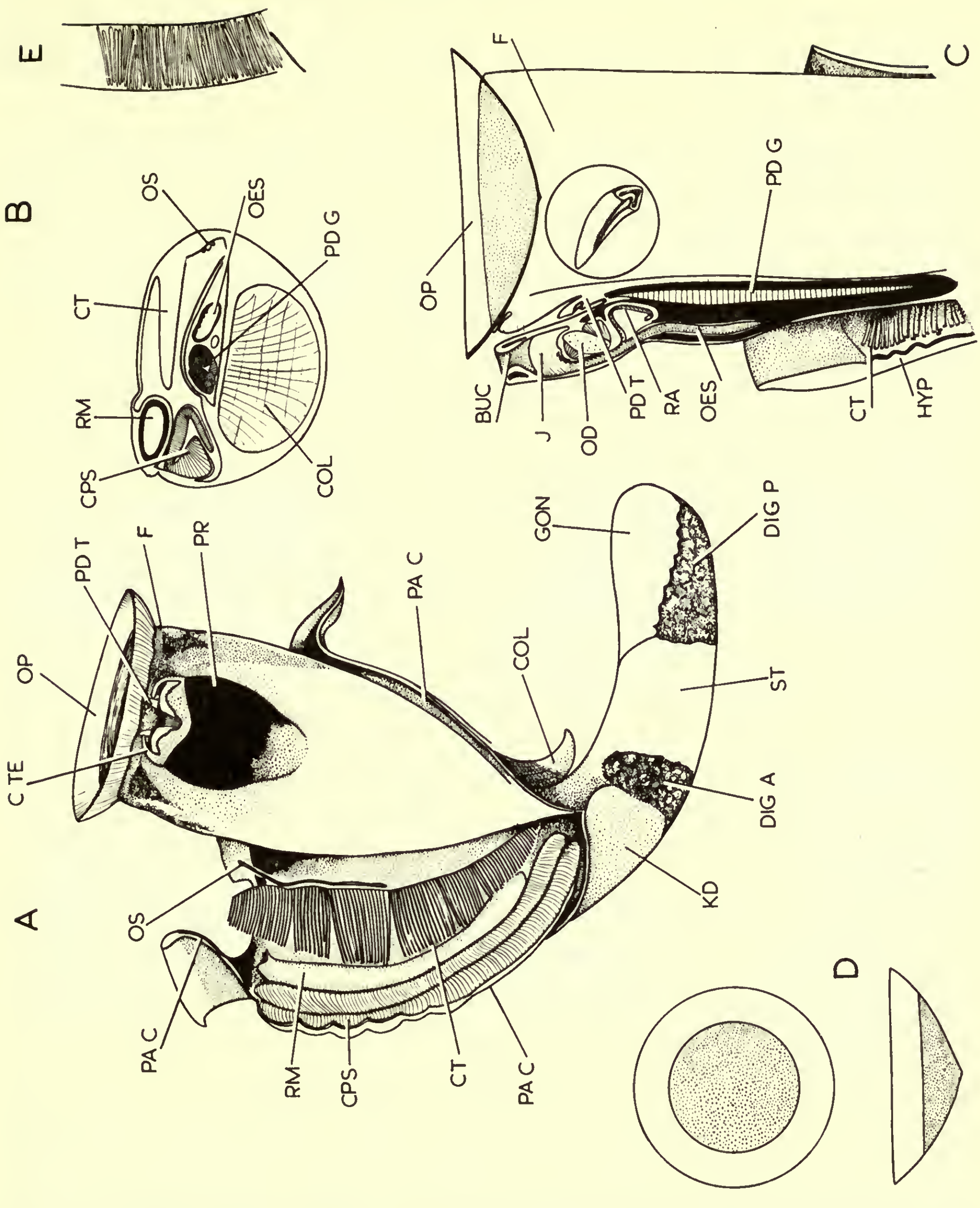
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Fig. 2. *Dendropoma maximum*. A. The entire female animal removed from the shell and with the mantle cavity opened along the right side, ventrally to the glandular genital tract. B. Diagrammatic transverse section through the pallial region. C. The head foot and mantle in sagittal section, showing the relative proportions of the parts for comparison with Text-figs. 9 and 3 for *Serpulorbis squamigerus* and *Dendropoma* (*Novastoa*) *lamellosa*. D. The operculum in external and in lateral view. E. Detail of the rectum showing the form of the faecal pellets.

D. irregulare and *D. ghanaense*, show an operculum externally convex, built up into a solid dome, and concave beneath where the axial mamilla emerges to form a plug inserted into the foot.

The dendropomatid operculum has the typical structure of a spirally wound band of chitin, in which by appropriate maceration—as in dilute caustic potash—the overlapping whorls may be dissociated as shown in Text-fig. 3D for *D. lamellosa*, leaving the more resistant mamilla at the centre. In opercula with a built-up dome, the successive coils of the chitinous band are strongly thickened, and of a mahogany red hue, narrowly triangular in section and superimposed to form a convex structure of great solidity. (See page 617 for discussion of the operculum in Vermetidae generally, and Text-fig. 15 for range of opercular structure in *Dendropoma*).[1]

On opercular characters the first and most primitive of the dendropomatids are probably among those with thin, concave, saucer-shaped opercula. In *D. marchadi* (Keen & Morton, 1960) the saucer is ornamented in its upward exposed concavity with an upstanding spiral lamina of two to three volutions. This character—not observed in any other dendropomatid studied—shows an affinity with the opercula of *Petaloconchus* and *Vermetus* s.s. *D. marchadi* has a tiny axial mamilla ; but in *D. maximum* this structure is generally lacking, being represented perhaps as a scarcely visible thickening of the chitin, at the bottom of the deep opercular bowl, which rests in a corresponding concavity in the muscular mass of the foot. The mamilla, though small, is quite obvious in *D. megamastum* while in the concave operculum of *D. lamellosum*, the mamilla forms a very large cylindrical peg running right through the operculum to appear freely above and below. It is flatly truncated on top, and underneath forms a round-tipped plug deeply inserted into the musculature of the foot. The mamilla shows the same deep foot insertion in the species with massively domed opercula ; but there the operculum is concave beneath and grips the muscular mass of the foot all-round. In these species, the mamilla does not emerge above but is smoothed off in the contour of the upper surface. Around the axial mamilla, the operculum in *D. irregulare*, *D. tholia* and *D. ghanaense* is built up of deep reddish-brown chitinous whorls, strongly thickened and opaque. The outermost whorl overspreads the edge of the foot in a reddish marginal zone ; outside that is a sharp peripheral lamella of transparent horn. For *D. irregulare*, the operculum of two stages of the non-adult is illustrated, showing the solid biscuit-shaped plate that is finally built into the convex dome.

The flat or but slightly concave opercula of *D. corallinaceum* and *D. rastrum* differ from either of the previous types by the rather papery thinness and irregularity of the projecting rim and the raised polished ring of thickened chitin upon the insertion surface. *D. corallinaceum* shows a small central mamilla. In *D. rastrum* there is no trace of this, and the upper surface has the successive whorls overlapping and irregularly jagged at the free margin.

In a previous paper, Keen & Morton (1960) have described the anatomy of a species of the concave opercular type (*D. marchadi*), and of one of the domed type

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[1] D'Arcy Thompson in "Growth and Form" (1942) (page 777) is incorrect in stating that the operculum of *Siphonium* (= *Dendropoma*) shows concentric growth and forms an exception to the general spiral rule

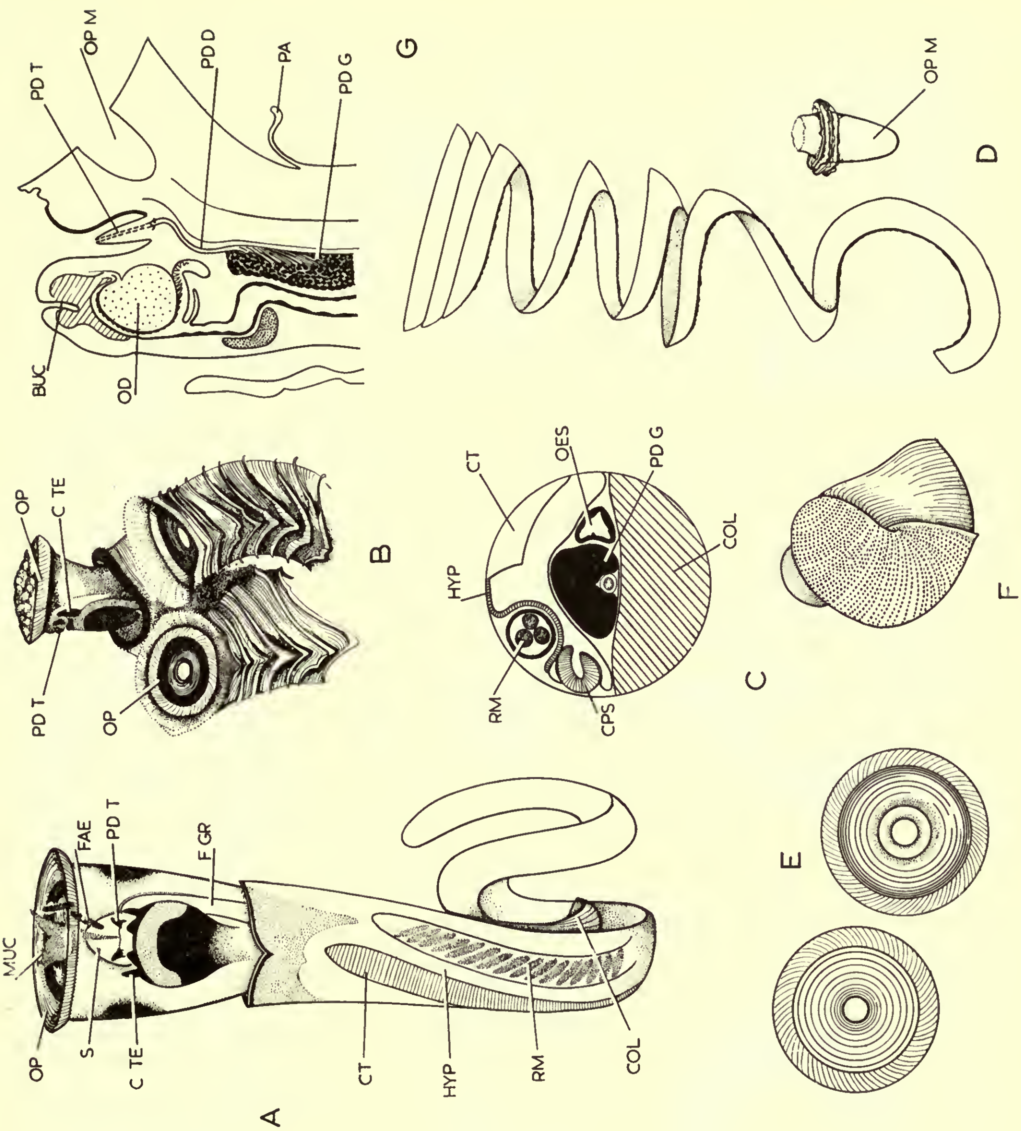
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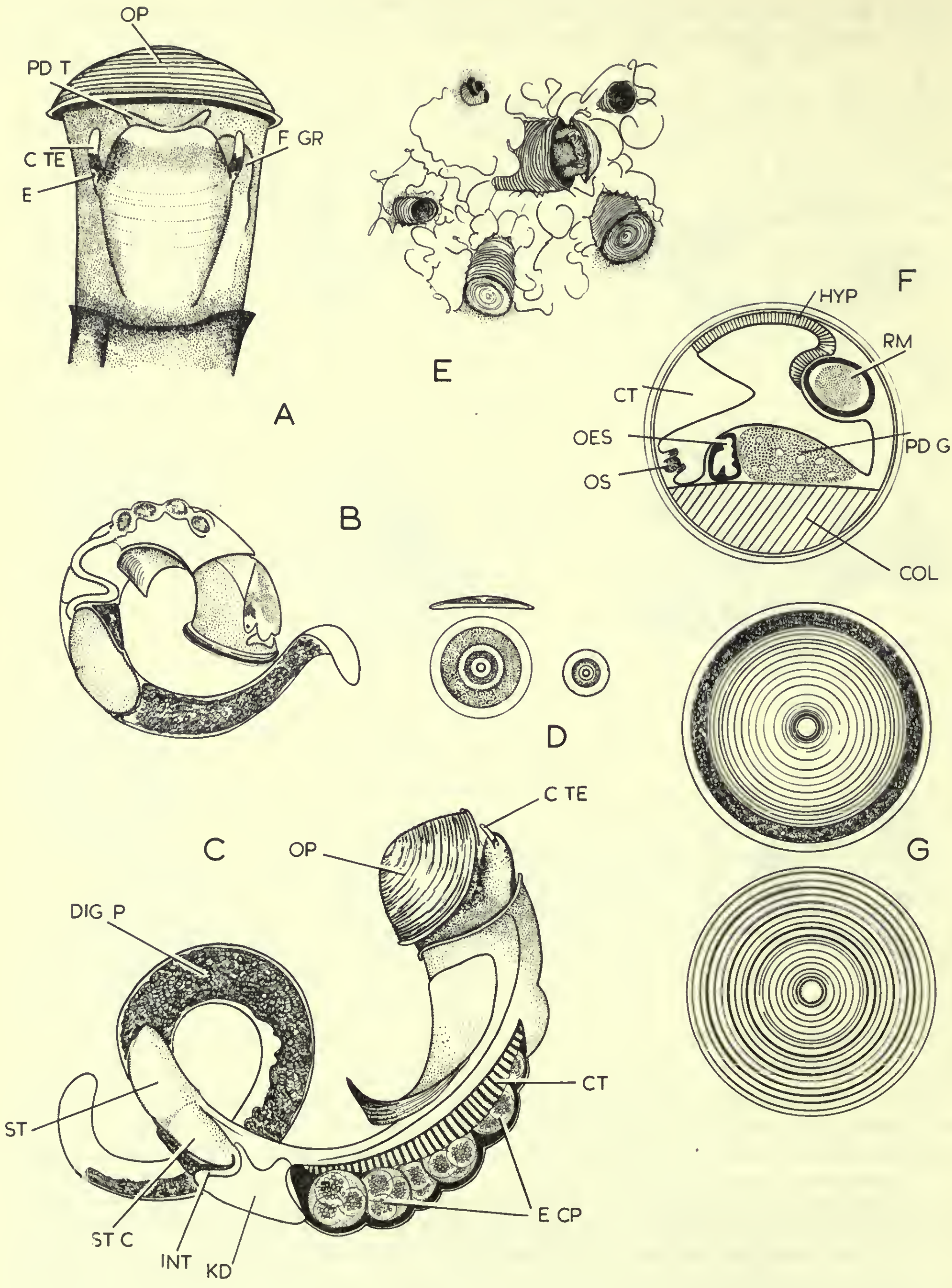
FIG. 3. *Dendropoma* (*Novastoa*) *lamellosa*. A. The entire animal removed from the shell and viewed from the dorsal surface. B. A cluster of animals showing one with the foot and head extended and the others withdrawn into the shells. C. Diagrammatic transverse section of the pallial region. D. The spirally wound strip of the operculum as displayed in extended view after maceration with caustic potash, and the axially mamilla separately shown. E. The operculum in inner (left) and outer (right) view. F. The embryonic shell with the beginnings of post-embryonic growth. G. The head and foot in sagittal section, showing the relative proportions of the parts, for comparison with Text-figs. 1 and 9.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(*D. tholia*). The mode of life and feeding mechanism has been described for *D. maximum* by Yonge (1932) and for *D. lamellosa* by Morton (1951a). Robertson (*in litteris*) has recently communicated observations on feeding in *D. irregulare*.

In most species of *Dendropoma* the body retains its primitive habit of growth, being wound in an open dextral gyre of several whorls, widening regularly from the apex. An operculum is never lacking and is always the most conspicuous feature of the animal viewed from outside, crowning the strong muscular plug of the foot. The operculum can be withdrawn only a short distance into the shell, as it closely approaches in diameter the widest and most recently formed section of the tube (see Text-fig. 3B for *D. lamellosum*). It serves effectively for the protection of the animal from attack, as it swiftly darts back to close the mouth of the shell. Deep retreat into the tube is precluded by the rather low insertion of the columellar muscle, that is, relatively near the head, marking the deepest point of attachment towards which the animal can be withdrawn.

In some species, as for example *D. irregulare*, the spire tends to have fewer whorls coiled in one or two widely open volutions, and in some specimens of *D. lamellosum* the distal part of the animal has a tendency to straighten out, as the latter part of the shell tube loses its original curved growth pattern. Sometimes, as in some adult specimens of *D. lamellosum*, the visceral spire may shorten abruptly after one or one-and-a-half turns and the top of the spire, formed by the digestive gland, is then bluntly truncated, the earlier parts of the shell being cut off by septa (see Keen, 1961, page 198). This tendency is carried furthest in *D. maximum*, by far the largest-sized species of the genus. As is evident from the work of Yonge (1932) on the anatomy of the animal, this is a species marked off in many ways from other Dendropomas (Text-fig. 2). As well as being very large, its shell forms in the adult a straight or only slightly curved tube. The body of the animal is thick and cylindrical, about the diameter of a man's small finger, with a short, blunt-tipped and only slightly curved visceral mass (Text-fig. 2A).

Both in the structure of the animal and in its exclusively ciliary feeding habits, the large-sized species *D. maximum* appears to fall furthest apart from other members of the genus. Its head and the exposed parts of the foot are handsomely pigmented in deep blue-black and light brown. The exposed mantle margin has a wide, blue-black band, and the operculum is of golden coloured translucent chitin. Much of the anatomy of the head and mantle cavity may be correlated with Yonge's description of the feeding habits of *D. maximum*. The head, as shown in longitudinal section in Text-fig. 2C, shows very different proportions in relation to the foot, from that of *Serpulorbis* species (see *S. squamigerus* for comparison) or even other species

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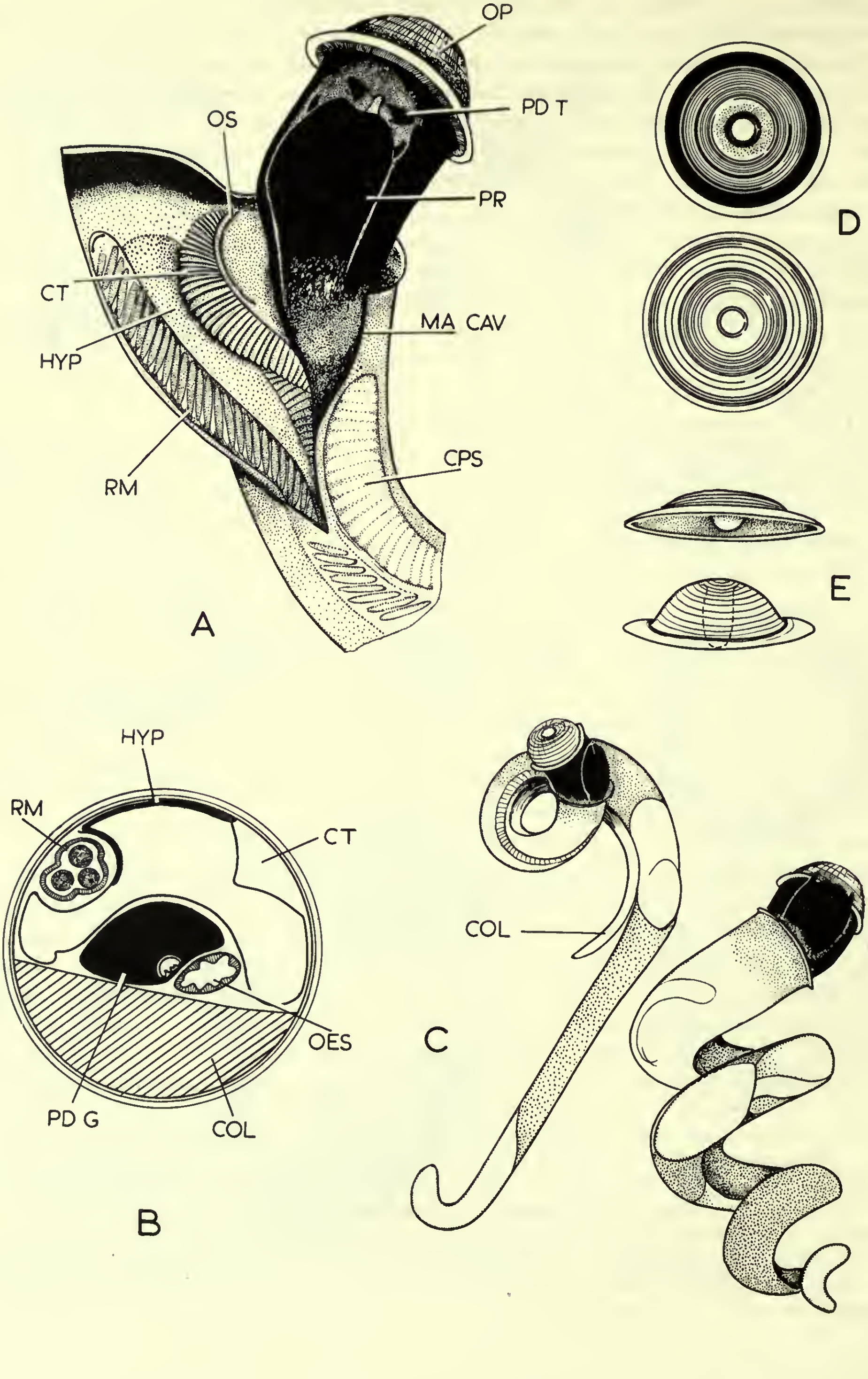
FIG. 4. *Dendropoma* (*Novastoa*) *irregulare*. A. Detail of the head and foot in dorsal view. B. A young animal taken from a recently attached shell. C. The whole female animal removed from the shell, with the mantle cavity opened to show the mode of carriage of the brood. D. Stages in the growth of the operculum in early settled animals. E. A group of specimens *in situ* showing the perforating habit of the shell, embedded in encrusting lithothamnion. F. Diagrammatic transverse section through the pallial region. G. The operculum, viewed (above) from within and (below) from the outer surface.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of *Dendropoma*. The head is much less massive than the foot and relatively shallow dorso-ventrally, with a buccal bulb of rather modest size. It appears likely that the size and muscular development of the buccal bulb are reduced in a ciliary feeder, which does not employ the radula for pulling back towards the mouth the heavy mucous traps extruded from the pedal gland of other species.

The pallial cavity contains by far the largest and best developed ctenidium seen in any vermetid investigated. The gill filaments have increased in length to form attenuated triangles, somewhat approaching to the parallel-sided and linear condition found in highly advanced ciliary feeders such as the Calyptraeidae (see Yonge, 1938). The filaments extend across the hypobranchial gland to conceal it completely from below, and they reach as far as the rectum on the right side of the pallial cavity roof. They have a ratio to the width of the pallial cavity of approximately 3 : 5. Yonge (1932, 1938) has described the action of the lateral ciliary fields in drawing a water current through the mantle cavity and of the frontal and abfrontal cilia in carrying collected particles to the tips of the filaments. These particles are projected from the tips of the gill filaments on to a ciliated tract on the right side of the mantle cavity floor. Here ciliary currents sweeping obliquely forward carry them to the neighbourhood of the right side of the head. Yonge (1932) identifies a weakly defined food groove forming a ciliated gutter at the right side of the head. From the preserved material figured here, this could not be separately detected (Text-fig. 2A). The particles brought to the front of the head by the cilia of the food groove come under the influence of mucus being extruded from the pedal gland, which embeds and binds the collected food, in preparation for its ingestion by the regular plucking strokes of the radula. The opening of the pedal gland is flanked by two short tentacles, carrying a ciliated groove along their medial edges. These tentacles are very short and slender ; in preserved material they usually curve inwards towards the centre line, although—as in other dendropomatids—they may diverge laterally in life. They appear to have the function of transporting or guiding the cone or small irregular mass of mucus that generally hangs from the mouth of the pedal gland, or rises from the surface of the foot in front of the mouth. The mucous mass is of smaller size in *D. maximum* than was figured in life for *D. lamellosa* by Morton (1951a), where it is suspected to be employed in direct mucous food collecting. With the reduced size of the mucous mass in *D. maximum*, we may correlate the reduction of the pedal gland (illustrated in transverse section in Text-fig. 2B and in longitudinal section in Text-fig. 2C). This has the smallest relative extent observed in any of the vermetids ; with a ratio of only 1 : 6 or 7 to the total body diameter, in contrast with the larger pedal glands, not only of *Serpulorbis* and *Petaloconchus* but also of other species of *Dendropoma*.

Of the mucus secreting sources within the mantle cavity, Yonge (1932) recognises

FIG. 5. *Dendropoma* " B " from West Africa (see Keen & Morton, 1960). A. The head, foot and pallial region of the animal removed from the shell and with the mantle cavity opened. B. Diagrammatic transverse section through the pallial region. C. Two views of the entire animal removed from the shell. D. The operculum from its inner face (above) and its outer aspect (below). E. Two oblique side views of opercula showing variations in height of the dome in different individuals.

an " endostyle " (so-called in the rather unsatisfactory terminology of Orton, 1914) running along the gill axis. Although in this part of the mantle wall mucus is probably diffusely secreted from the general integument, there appears to be no such highly specialised endostylar tract, with well demarcated zones of secretory and ciliated cells, as has been described for the ciliary feeding families Calyptraeidae (Orton, 1912), Struthiolariidae (Morton, 1951), and Siliquariidae (Morton, 1951a).

In the remaining and smaller-sized species of *Dendropoma* the pedal gland is in every case better developed. The transverse sections of the pallial region illustrated for *D. irregulare, D. tholia* and *D. lamellosum,* show a large pedal gland, semicircular in section, bulging through the pallial floor and massively displacing the narrower oesophagus to the left side. Morton (1951c) has suggested that mucus contributes to food collecting in *D. lamellosa* and Keen & Morton have advanced the same view for *D. tholia* and *D. marchadi.* More recently, Robertson (*in litteris*) has given a useful account of feeding in *D. irregulare,* and has kindly allowed me to quote in anticipation of a more detailed account by him. " Mucus produced by the enlarged pedal gland is formed into threads and spread out radially from the aperture of the shell with the pedal tentacles. Plankton, organic detritus and numerous sand grains in suspension are entangled and the threads are then drawn into the mouth with the radula."

The pedal tentacles in *Dendropoma* species are, however, seldom larger or much more prominent than in *D. maximum.* They remain short, club-shaped or pointed processes, well hidden beneath the tip of the snout and the rim of the operculum. Only in *D. marchadi* do they appear—from preserved material—to be longer and more mobile. With respect to the elongation of the gill filaments, the only other species found during my own work to show any tendency to the form shown in *D. maximum* is *D. marchadi,* where they are narrowly triangular, with a ratio of slightly more than 1 : 2 to the diameter of the mantle cavity. In *D. irregulare, D. tholia,* and *D. ghanaense* they are typically triangular, with no trace of elongation. In *D. lamellosa* the filaments are especially short, forming broadly based triangles, seemingly ill-adapted for ciliary food collecting. Neverthless, both the species, *D. lamellosum* and *D. irregulare,* investigated living, show some ability to feed by ciliary means with the ctenidium. A well-developed ciliated food tract runs along the right side of the mantle cavity floor in *D. lamellosum* carrying particles bound in mucus for ingestion at the mouth. *D. tholia* has a food tract lined with thickened ciliated and mucus-producing epithelium, well demonstrated in sections. Of *D. irregulare,* Robertson states that there is a broad ciliary tract on the right side of the animal which carries particles gleaned from the ctenidium forward to the mouth. Though some food is obtained in this way the amount is held to be small.

From the study of fixed material alone, in spite of the unspecialised appearance of the gill filaments, or the apparent small size of the pedal tentacles, it must be unsafe to exclude the possibility of either type of feeding habit. Judgment must be reserved until living material may be examined ; and we must keep in mind the probability that both ciliary and mucous methods of food collecting may frequently be employed together.

The transverse sections of the pallial region in *Dendropoma* illustrate also the mode of incubation of the eggs and the disposition of the female genital duct (Text-figs. 1A, 2B, 3C). The mantle margin of the female is always entire in the dorsal mid-line, never slit backwards as in *Serpulorbis* or *Vermetus* ; and the egg capsules are never attached to the shell but are carried in the mantle cavity in a single row of up to 12, as in the smaller sized *D. tholia* or *D. irregulare,* or in a double row as in the larger *D. marchadi.* Such a simple incubation method is only compatible with the lack of deep retreat of the animal into the upper reaches of the tube ; the eggs can here be held freely in the mantle cavity without risk of sudden crushing during emergency withdrawal of the animal into the tube. For *D. maximum* we have as yet no information either about the mode of brood carrying or the form of the embryonic shell. With the extrusion of a long line of egg capsules directly into the mantle cavity in *Dendropoma,* the long distal section of the female genital duct, the capsule gland, runs as a glandular furrow of uniform width for most of the length of the pallial cavity. It lies immediately to the right of and ventrally to the rectum, and—as may be seen from the sections—it forms a thick-walled trench open along its whole length. Its extended slit-like aperture offers a more extended entry to current-borne sperm, (the male vermetid is aphallic), and allows the emergence of a long row of egg capsules placed end to end throughout the mantle cavity. In *D. maximum* the capsule gland is especially elongated, and contiguous with the whole ventral aspect of the rectum.

The digestive system appears to provide no distinctive generic features for *Dendropoma.* A typical vermetid stomach has been described (Morton, 1951a) for *Serpulorbis zelandicus.* This shows a close agreement in the relations of style sac, gastric shield, sorting area and digestive diverticula, with the stomachs of *Dendropoma lamellosum* (Morton, 1951a) and of *D. maximum,* described by Yonge in 1932.

The radula has a characteristic appearance for the genus *Dendropoma* (see Text-figs. 13A–F). The general form of the median tooth is rectangular, somewhat wider in the transverse dimension, with posterior corners built out into short, curved, horn-like flanges. These are fairly strongly chitinized and fit into concavities on the lateral teeth. The lateral teeth are as typically in vermetids, with their main cusp as long as the median cusp of the central, with three smaller cusps laterally to it. The first marginal tooth bears at either margin two low cusps and towards the tip a stronger spine-like cusp directed terminally. The second tooth is smooth save for a similar spine-like cusp.

(ii) Genus ***PETALOCONCHUS***

Species examined:

1. *P.* (*Macrophragma*) *montereyensis* (Dall, 1919) ; California.
2. *P.* (*Macrophragma*) *nigricans* (Dall, 1919) ; Florida.
3. *Vermetus* (*Thylaeodus*) *contortus* (Carpenter, 1857) ; Tropical West America (see Keen, 1960, p. 201). B.M. (N.H.) Reg. No. 57.6.4.1490.

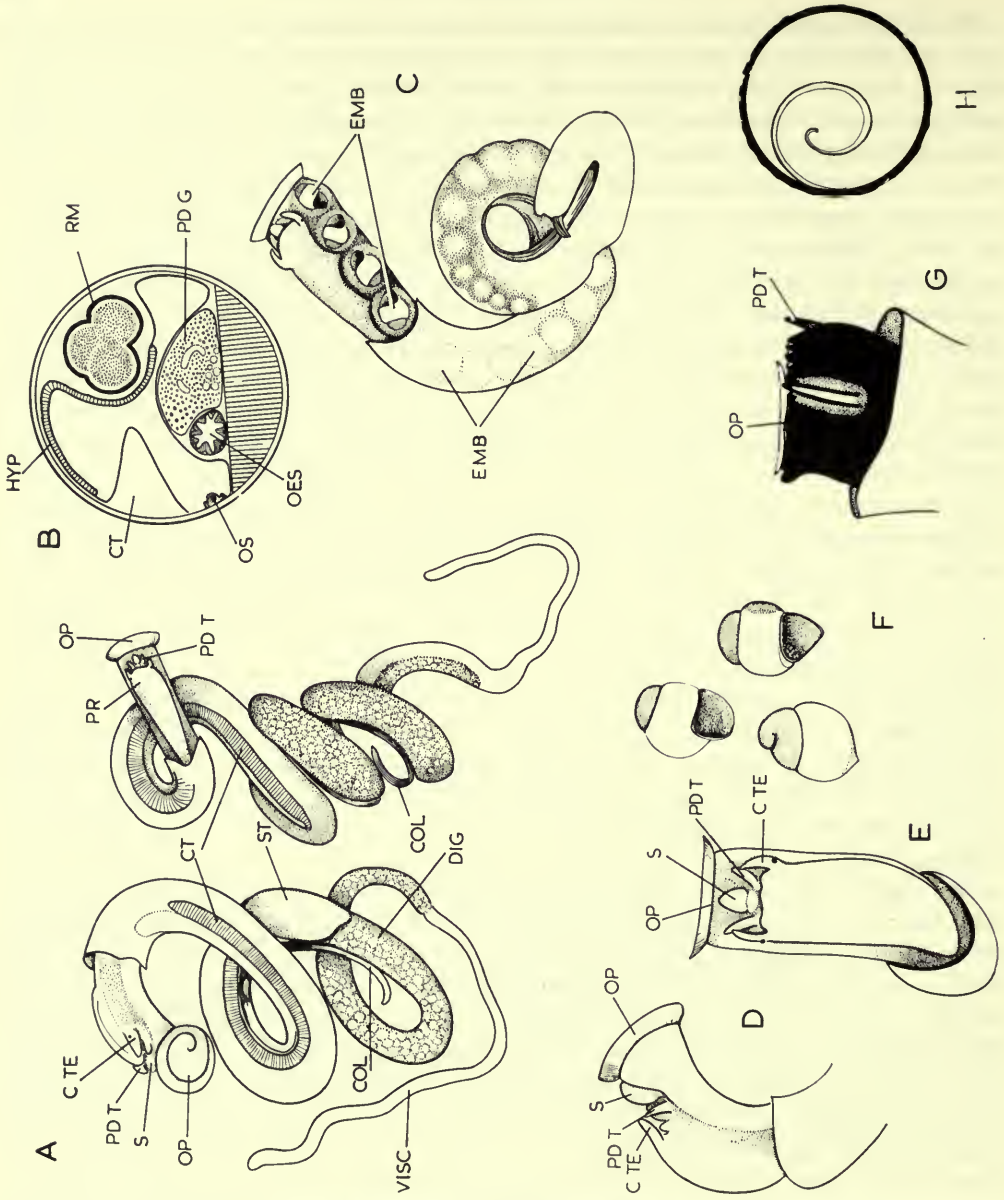
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Fig. 6. A–F *Petaloconchus montereyensis*. A. Two views of the entire animal with the head shown (left) from the left side and (right) in dorsal view. B. Diagrammatic transverse section through the pallial region. C. Female animal showing the location of the eggs and shelled embryos within and in front of the mantle cavity. D. Detail of the head and foot in right side view. E. The head and foot in dorsal view. F. Embryo shells shortly before liberation.

G–H *Petaloconchus nigricans*. G. The head, foot and operculum from the left side. H. The operculum in surface view.

The chief diagnostic feature of the genus *Petaloconchus* is shown by Keen (1961) to be the development in the earlier part of the tube of a pair of spiral lamellae of varying complexity, partly subdividing or restricting the space occupied by the animal. In addition, the subgenus *Macrophragma* (the *Petaloconchus* of most authors, to which belong the great majority of the species, including *P. montereyensis* and *P. nigricans* examined here) is characterized by a distinctive coiling pattern, the whorls being laxly superimposed on each other like a " Turritella squeezed sideways " to quote Carpenter's description. The nucleus too is strongly diagnostic, having 2–4 whorls, more than in *Dendropoma*, but being of smaller actual size. It is never brown, but ivory white to waxy yellow in colour, and conical to rather distinctively cylindrical or barrel-shaped in outline (see Text-fig. 6F). The operculum is always present, though never so elaborate as it may become in *Dendropoma*. It is shallowly concave with an upstanding spiral lamina of one or two volutions. Though it generally covers the foot and may slightly overspan the sides, it is always considerably smaller than the diameter of the aperture.

Species of *Petaloconchus* are seldom of great size as compared with the largest of *Dendropoma* or with a typical *Serpulorbis* ; the body of the animal when removed from the shell is found to be long and extremely slender, having the general appearance of the sideways displaced spiral coils of the shell. In *P. montereyensis*, which has a very typical development of internal spiral lamellae, these greatly restrict the internal diameter of the earlier whorls of the adult tube. The body of the animal is produced to a long tail, of uniform thickness of about half the rest of the body, and running right through the part of the shell occupied by the lamellae. This tail appears to consist wholly of gonadial tissue displaced backwards from its usual site alongside the digestive gland. The columellar muscle (see Text-fig. 6A) is of very different shape from that of *Dendropoma* ; it is attached far back in the shell at a depth of at least two full volutions, alongside the visceral mass of the animal, and forms an attenuated narrow strip running for a good distance free of the rest of the body. Such an arrangement equips the animal for a deep protective retreat into the shell. Unlike that of *Dendropoma*, the operculum is scarcely massive enough to serve for protection and is somewhat too narrow to close the aperture. In my specimens of *P. nigricans* it does not in fact cover the whole top of the foot.

The exposed parts of the head and foot are jet black in *P. nigricans* with the cephalic tentacles long and ornamented with a lighter stripe. The inner surface of the mantle skirt is also broadly black edged. In *P. montereyensis* the animal in spirit is yellowish white or pale-coloured, with no prominent pattern or colour markings. The operculum in *P. montereyensis* (Text-fig. 6D) is a thin concave saucer, bearing a spiral lamina in its concavity and strongly overlapping the sides of the foot. The head and the proboscis do not appear to show the massive size sometimes found in *Serpulorbis*, and the head and foot present no special features very unlike those of *Dendropoma*. The pedal tentacles lie beneath the proboscis, being somewhat longer than the cephalic tentacles in preserved material, and forming incurved or divergent papillae, with a small, pale-coloured patch of integument between them that represents the sole of the foot. Despite the small size of the pedal tentacles, the pedal mucous gland, as illustrated for *P. montereyensis*, is of very large size. It extends backwards for the whole length of the mantle cavity (about half that of the entire animal) and bulges strongly through the mantle cavity floor as a thick, dorsally convex, glandular strap.

The considerable size of the pedal mucous gland suggests that its secretion must clearly be employed for the formation of mucous traps, though there is no such pronounced development of the pedal tentacles as in *Vermetus* s.s. and in *Serpulorbis*. Robertson (*in litteris*) describes a similar mode of mucous feeding in *P. nigricans* to that observed in *D. irregulare*. The mucous threads are as long as 12–15 cm. The pallial cavity has no clearly defined food groove, but its forward ciliary currents on the right side are stated to be stronger than in *D. irregulare*. The gill filaments are equilaterally triangular in shape. A ciliary method of food collection, by the action of the gill and the ciliated tract, must supplement the action of the mucous traps, particularly at times when the erect apertural tube of the shell is broken off and repaired, the rest of the tube being meanwhile almost closed by a thin convex shelly septum, rendering the deployment of mucous traps impossible.

The genus *Petaloconchus* has been little studied in life, and as with *Dendropoma*, an investigation of the feeding habits of some of the fairly easily available American species would be highly rewarding.

The arrangements for the retention and brooding of the eggs in *Petaloconchus* hardly appear to differ from those of *Dendropoma*. The mantle skirt is entire, being never slit in the middle line in the female, and the eggs and embryos are retained in a row extending backwards for the whole length of the mantle cavity, those furthest forward being the most advanced in development. Text-fig. 6C for *P. montereyensis* illustrates the mode of carriage of the eggs and embryos ; and Text-fig. 6D shows the form of the embryonic shell. The oldest embryos at the front of the row, lying against the head, have not yet attained their full number of whorls, as found in the finished embryonic shell ; it would be interesting to discover whether the veliger acquires its extra whorl during a final interval of free-swimming, after the conclusion of incubation and before settlement. (Cf. the mesogastropod *Struthiolaria* (Morton, 1951) for a similar succession of an incubatory phase by a short free-swimming episode.) The capsule gland of the female *Petaloconchus* forms a long, thick-walled trench, with an extended opening, much as was found in *Dendropoma*.

In any consideration of the genus *Petaloconchus* the status of the small, slender-tubed species, *Vermetus contortus* of Carpenter (1857) falls to be assessed. This Southern Californian species was first regarded by Dr. Keen as a *Petaloconchus*, but was later removed into the subgenus *Thylaeodus* of Mörch (1861) under the genus *Vermetus* s.l., on account of its lack of internal spiral laminae. The operculum (see Text-fig. 7E) is characteristically that of a *Petaloconchus*, slightly overlapping the sides of the foot though not reaching the diameter of the aperture. It carries in its shallowly concave upper surface a spiral flange of one-and-a-half volutions. The embryonic shell too is typical of *Petaloconchus* as characterized by Keen (1961).

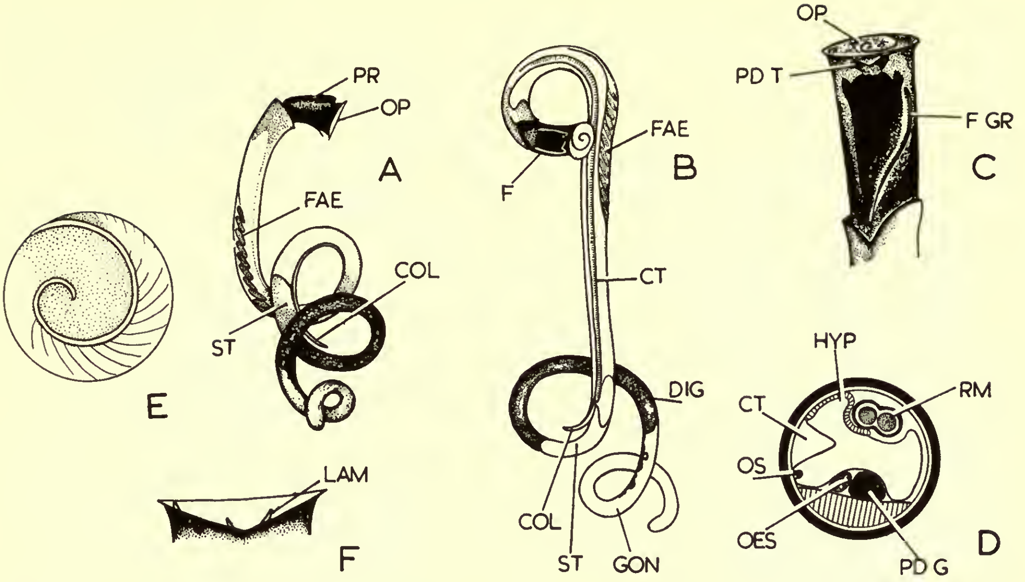

Fig. 7. *Vermetus* (*Thylaeodus*) *contortus*. A, B. Two views of the whole animal removed from the shell. C. The head and foot in dorsal view. D. Diagrammatic transverse section through the pallial region. E. Operculum in surface view from above. F. Diagram of the operculum in position upon the foot in sectional view.

Dr. Keen finds the conchological distinction between *Thylaeodus* and *Vermetus* s.s. slight and predicts that the separate groupings may be unjustifiable. The animal of Carpenter's *contortus* is illustrated here (Text-fig. 7) ; and as a result of this investigation, it would appear to have little in common with either of the other two species referred to *Vermetus* s.s., including the type *adansonii*. Except for its neglect to develop internal lamellae and the consequent narrow " tail ", Carpenter's *contortus* has every other qualification needed for *Pelaloconchus*, such as the conic-cylindric character of the nucleus, the " squeezed sideways coiling pattern ", and the narrow body with the columellar muscle forming a long slender strip stretching far back to allow deep insertion within the tube. The pedal tentacles are small, dark-pigmented, divergent papillae, and the whole of the exposed head and foot are black-pigmented. The pedal gland, as shown (Text-fig. 7D) in cross section of the pallial cavity, is massive and semicircular in section. The operculum differs by its large size from the spirally laminate one of *Vermetus* s.s. which is always a vestigial button.

The radula of *P. contortus* moreover agrees with that of *P. montereyensis* and departs from that of other genera ; it is strikingly different, for example, from that of *V. adansonii*. The central tooth in *Petaloconchus* is a transverse rectangle, wider in its cross dimension, and with side projections or peg-like lobes similar to those of *Dendropoma* but somewhat stronger and more peg-like. The lateral teeth are much as in *Dendropoma* or *Serpulorbis*. The first marginal tooth shows—as

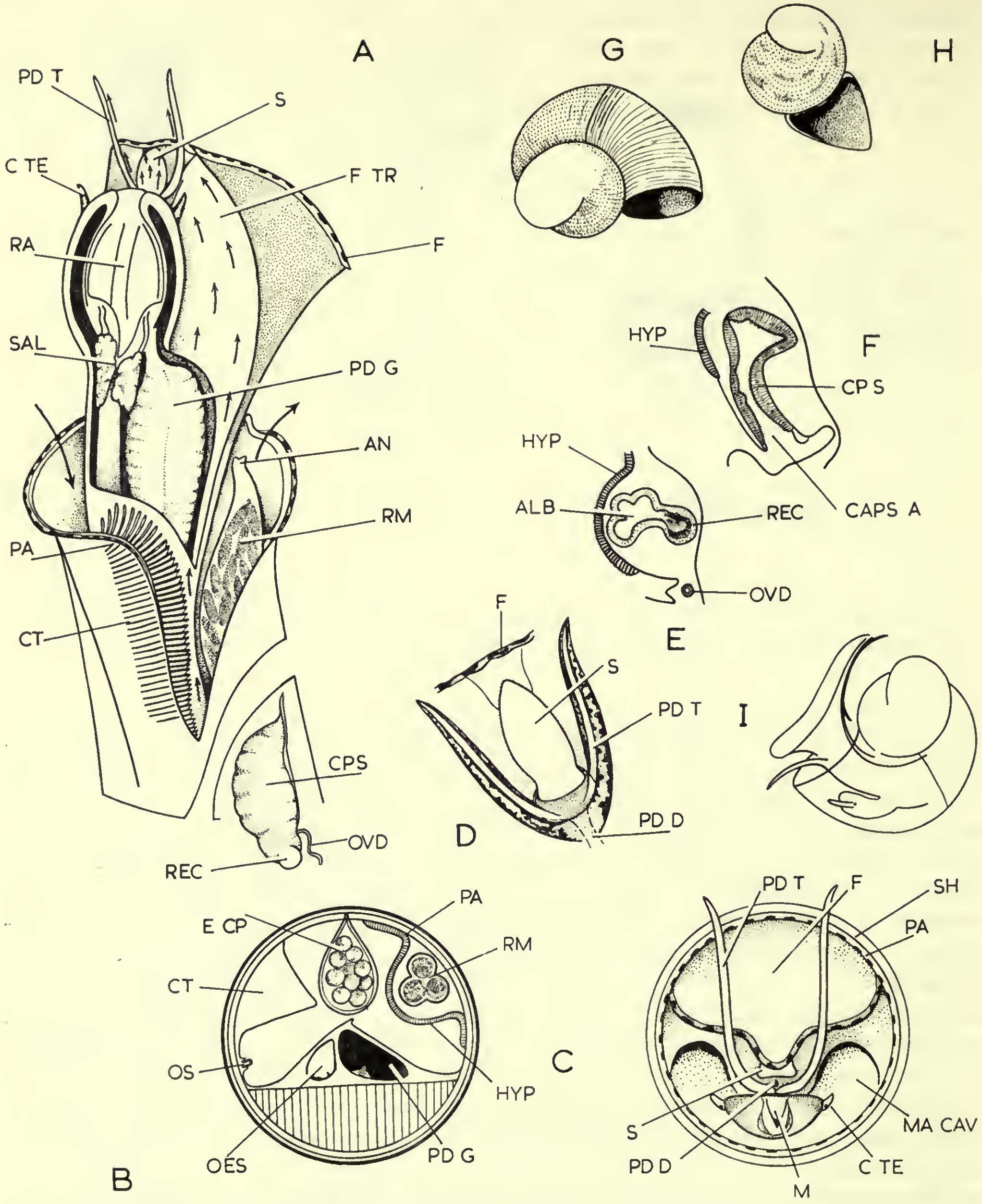
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Fig. 8. *Serpulorbis zelandicus.* A. Head, foot and pallial cavity of the female. The pallial cavity is shown without dissection, as viewed through the median slit. The body wall of the proboscis and of the head immediately behind it has been dissected to show the internal structures. The arrows indicate ciliary currents within the mantle cavity. B. Diagrammatic transverse section through the pallial region. C. The head and foot as partly retracted within the pallial cavity, viewed looking down upon the shell aperture.

well as the distally-directed spine-like cusp—a row of four or five weaker cusps on either margin a little further back. The second marginal tooth, which is smooth in *Dendropoma* except for its spine-like tooth, has in *Petaloconchus* a row of four or five weak cusps at either side.

(iii) Genus ***SERPULORBIS***

Species examined :

1. S. (*Serpulorbis*) *gigas* (Bivona-Bernardi, 1832) ; Mediterranean.
2. S. (*Serpulorbis*) *squamigerus* (Carpenter, 1857) ; California.
3. S. (*Serpulorbis*) *zelandicus* (Quoy & Gaimard, 1822) ; New Zealand.
4. S. (*Serpulorbis*) *aotearoicus* Morton, 1951 ; New Zealand.

By comparison with either *Dendropoma* or *Petaloconchus*, any species of *Serpulorbis* presents a number of differences in the outward appearance of the animal, which at once set it off as easily referable to this genus. First, there is no operculum, and the flat top of the foot is soft and often brightly coloured. The disc of the foot is highly sensitive to tactile stimuli and its margin is very labile and deformable by small local muscular contractions. The foot musculature appears much less solid than in the firm cylindrical plug which bears the operculum in *Dendropoma ;* and the head and proboscis, containing a very large buccal mass, are much more massive in proportion to the foot as compared with *Dendropoma*, especially with the species *maximum*. That this is a real difference of proportion, even allowing for the greater shrinkage upon preservation of the foot, where its shape is not maintained by the hard operculum, is amply apparent from comparison of the animals in life. The greater massiveness of the buccal mass in a predominantly mucous feeding group is probably to be attributed to the important function of the radula in hauling back for ingestion the quite extensive mucous sheets or traps.

The second obvious feature of *Serpulorbis* is the generally much greater prominence of the pedal tentacles. These are no longer inconspicuous appendages at the opening of the pedal gland, but are very long, attenuated filaments, standing erect above the front edge of the foot and no longer overshadowed by the brim of an operculum. The cilated groove on their mesial side runs from the opening of the pedal gland to the tentacle tip. Besides being sensitive tactile structures the pedal tentacles seem to be chiefly responsible for deploying the mucous strings in *S. zelandicus*, *S. aotearoicus*, and *S. gigas*. The pedal tentacles of *S. gigas* are deeply incised by their mesial ciliated groove ; they curve outwards in horseshoe shape from the aperture of the pedal gland, and may be extended a good deal further than the figure by Yonge & Iles (1939), or my Text-fig. 10F, of retracted tentacles, would

D. Detail of the sole of the foot, the opening of the pedal gland and the pedal tentacles, somewhat more contracted than in A. E, F. Transverse sections of the female genital duct at a posterior level (E) through the albumen gland and more anteriorly (F) through the capsule gland. G. The embryonic shell with the first portion of the post-embryonic tube already formed. H. The embryonic shell taken from one of the capsules within the mantle cavity. I. Early post-embryonic stage, showing the temporary operculum

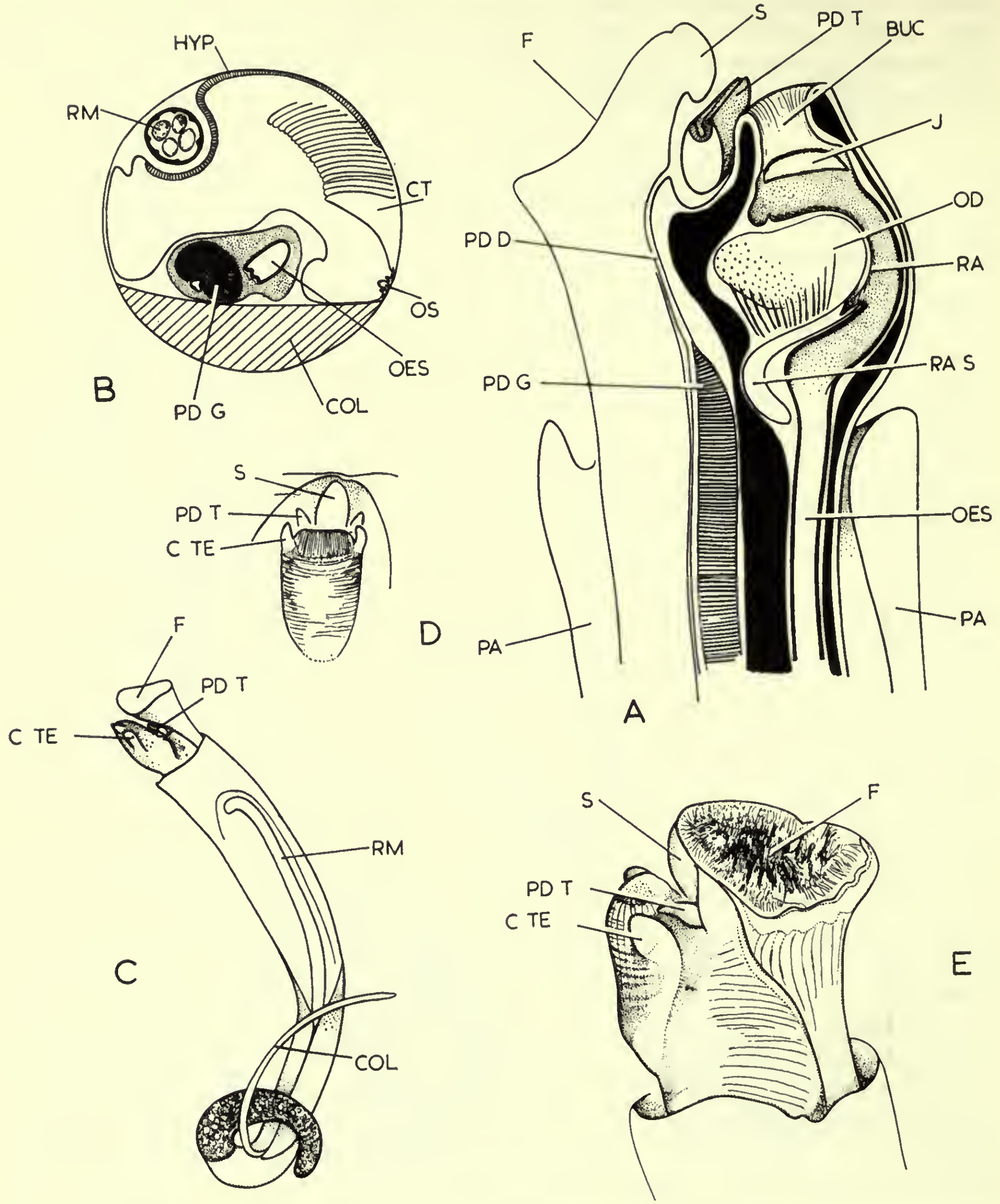
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FIG. 9. *Serpulorbis squamigerus*. A. Diagrammatic sagittal section of the head, foot and mantle cavity for comparison with Text-figs. 1 and 3, of *Dendropoma* (*Novastoa*) *lamellosa* and *Dendropoma maximum*. B. Diagrammatic transverse section through the pallial region. C. The entire animal removed from the shell and viewed from the right side. D. Detail of the head, sole of the foot and pedal tentacles from above. E. Detail of the head and foot from the right side.

suggest. The smaller size of the pedal tentacles in my specimen of S. *squamigerus* must to some extent be a preserving artefact ; Johnson & Snook (1935) show them, for example, much longer than in any observed *Dendropoma* or *Petaloconchus*, though relatively shorter than in S. *gigas* or S. *zelandicus*. This may perhaps be

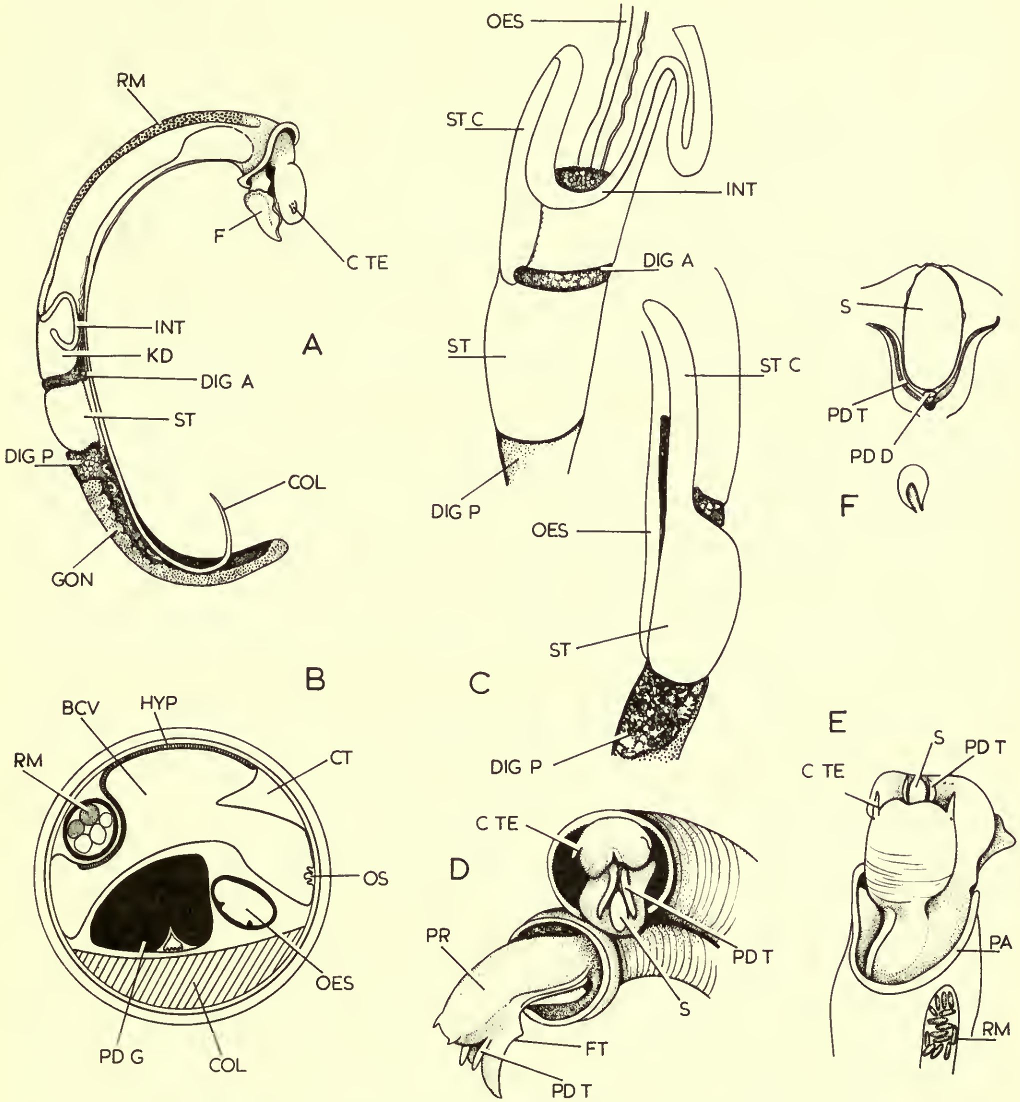
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FIG. 10. *Serpulorbis gigas*. A. The entire animal removed from the shell and viewed from the right side. B. Diagrammatic transverse section through the pallial cavity. C. The stomach, style sac and intestine, viewed from the left side (below) and the right side (above). D. Two animals with the head and foot partly extended from the shell. E. Detail of the head and foot viewed from above. F. Detail of the sole of the foot. and the aperture of the pedal gland with the pedal tentacles (one shown in section).

correlated with the habit of *S. squamigerus* of constructing a communal mucus sheet serving as a " mess-table " for an agglomeration of animals, rather than deploying individual mucus strings by means of the pedal tentacles (see MacGinitie & MacGinitie, 1949).

With the loss of the protective operculum, the foot takes on a variety of bright colours, and these are shared by the head and proboscis and the widely exposed rim of the mantle, extending freely over the margin of the shell. Yellows, reds and blacks appear to predominate (see Morton, 1951a for the New Zealand species). In *Dendropoma* species also there is a preponderance of jet black on these parts of the body, relieved at the mantle and tip of the snout and tentacles by either yellow or red. It may not be too fanciful to suspect that these conspicuous colours are aposematic ; comparison may be made with the Nudibranchia (Garstang, 1890), where a naked skin surface assumes an array of bright colours, and is accompanied by distasteful properties to predators (Thompson, 1960).

The chief means of protection available to the animal of *Serpulorbis* is, however, by deep retreat into the shell tube which can be effected with lightning rapidity when the animal is disturbed. This habit has its effect in the design of many of the parts of the body enclosed within the tube. First, the body of the animal when removed from the shell is quite limp, and can only be described as vermiform ; it lacks any permanent or well-defined spiral configuration. The columellar muscle does not as in *Dendropoma* form a short, broad strap lending its shape to the overlying body, but for the most part runs free of the body as a long, narrow slip inserted very far back in the shell, often at the level of the tip of the visceral spine (see Text-fig. 9C). This position of attachment allows a long retraction of the animal, and the limpness of the body facilitates its passage through the often irregularly wound volutions of the shell.

Deep retreat into the narrower reaches of the shell is made possible by the lack of an operculum and the extreme compressibility of the soft foot. Compression of the mantle cavity, or the withdrawal of the head and foot into it, would not, however, be possible with the egg capsules lying freely within the mantle cavity as in *Dendropoma* and *Petaloconchus*. The capsules are instead attached to the interior of the shell, shortly within the mouth (see Text-fig. 8B). The mantle of the female is slit backwards in the median line along the line of attachment of the row of capsules (see p. 621).

The principal trend shown by the pallial organs in *Serpulorbis* is the reduction in the size and functional importance of the gill, more especially in those exclusively or predominantly mucous trap feeders such as *S. gigas*, and *S. squamigerus* that form the most advanced section of the genus. The gill filaments in all species examined are equilaterally triangular, and—although the gill extends the whole length of the mantle cavity—it may become extremely narrow, the filaments having in *S. gigas* a ratio of only 1 : 5 to the total diameter of the mantle cavity. In *S. squamigerus* and *S. gigas* the ctenidium appears to be partly enclosed in a separate narrow compartment on the left side of the mantle cavity by the tendency to develop a high longitudinal ridge down the median line of the mantle cavity floor. Correlated with the importance of mucous trap feeding, the pedal gland like the pedal tentacles, in *Serpulorbis* reaches its greatest development among the Vermetidae.

The earliest and fullest account of mucous trap feeding in *Serpulorbis* is that of Boettger (1930) for *S. gigas*. The pedal gland and the action of the pedal tentacles have been well described for the same species by Yonge & Iles (1939), who provide a detailed comparison with the same organs in *Dendropoma maximum* under the name of *Vermetus novae-hollandiae*. The same structures are described and illustrated by me for *S. aotearoicus* (Morton, 1951a). The typical appearance of the pedal gland in transverse section is shown in Text-fig. 6B, my Fig. 4 (1951a) being drawn too far posteriorly to represent adequately the bulk of the gland.

In *Serpulorbis gigas*, dependent entirely on mucous traps, long ropes are put out, reaching more than a foot in length, and become loaded with planktonic organisms before being pulled back and grasped by the radular teeth and by the pair of sharp-edged jaws. The pedal tentacles evidently assist in carrying the extruded mucus upwards and clear of the body as it is put out from the pedal gland and formed into the feeding trap. The tentacles may also have a manipulatory power over the spread out mucous cone or threads, and may assist in hauling it in when it is loaded with food for ingestion.

The colonial species *Serpulorbis squamigerus* (see MacGinitie & MacGinitie, 1949) makes a different use of mucus : here a communal sheet of mucus is contributed by the glands of many individuals and the food caught up in it is afterwards ingested as portions of the sheet are plucked off by the radulae of the separate animals.

In *S. gigas*, the gill reaches the smallest proportions found in any vermetid examined, with the exceptions of *Vermetus adansonii* and *V. triqueter*, where it has suffered equal reduction. *Serpulorbis squamigerus* has a somewhat wider gill, with filaments of greater area ; this fact is perhaps related to the need to draw in the pallial water current through the loose mucous meshwork of the overlying communal feeding table in a way that cannot be required with the longer and loosely deployed mucous traps of *V. gigas*.

Despite their unspecialized triangular gill filaments, and the lack of the further refinements of ciliary feeding adaptations, it is clear that some serpulorbids resort to a considerable degree of ciliary feeding along with the use of mucous traps. Thus in *S. aotearoicus* and *S. zelandicus* slender mucus strings are sometimes found issuing from the pedal gland but are generally elusive and difficult to observe. In these species, the triangular gill filaments are relatively well-developed for a *Serpulorbis*, drawing a current into the mantle cavity by powerful lateral cilia. Frontal cilia carry particles towards the right side of the mantle cavity, where they are projected off the gill on to a smooth, wide tract of the pallial cavity floor, sweeping round the right side of the foot to the neighbourhood of the mouth. This has powerful anteriorly-directed cilia, and uniformly tall mucus-secreting epithelial cells. The more general mucus source, the hypobranchial gland, is still present upon the roof of the mantle cavity to the right of the gill, but does not seem to be peculiarly or at all closely associated with feeding. On the other hand, the gill axis bears no " endostyle " so-called, of the kind developed in more specialized ciliary feeders, lacking the pedal mucous gland (i.e. Crepidulidae, Siliquariidae and Struthiolariidae). The long and slenderly tapering pedal tentacles in all species of *Serpulorbis* rise well above the level of the terminal disc of the foot. They can be freely moved about as sensitive tactile and exploratory organs, being much larger and more active than the head tentacles which are raised towards the tip of the bulbous snout ; the chief tentacular sensitivity is thus shifted from the head to the new food-getting region, which is the part of the foot in the vicinity of the pedal gland aperture.

The female genital ducts of *Serpulorbis zelandicus* were described by Morton (1951a). The ovarian duct opens into a proximal albumen gland to which is attached a pouch-like receptaculum seminis. The capsule gland is no longer as in *Dendropoma* a thick-walled groove prolonged the length of the mantle cavity, but a purse-shaped sac, open by a slit upon its longer side, and able at one time to secrete and place in position on the shell a single capsular envelope.

(iv) Genus ***VERMETUS*** s.s. Daudin, 1800

Species examined :

1. *V.* (*Vermetus*) *triqueter* (Bivona-Bernardi, 1832) ; Mediterranean.
2. *V. adansonii* Daudin, 1800 ; West Africa.

Preserved animals of the type species, *Vermetus adansonii*, Adanson's original " le vermet ", have been collected and kindly presented to Dr. Keen and myself by M. Marche-Marchad, from the type locality, Senegal, French West Africa. Three specimens examined after careful soaking out from the dried state gave a clear indication of the anatomical features necessary for generic assignation, though rather few of the finer histological details. For *Vermetus triqueter* I have had fixed material collected at the Oceanographic Institute, Monaco ; and have also had much help from the description and figures of Lacaze-Duthier's memoir of 1860 which, couched in the convention of another age, are beautifully detailed and clear and go unerringly to the features still of salient interest to the student of a century later.

Both these species have a profound resemblance to *Serpulorbis* in the features of the animal ; and were it not for their vestigial operculum mounted on the disc of the foot, there would be few if any malacological objections to throwing *Serpulorbis* into Adanson's original genus *Vermetus*.

The body of *V. triqueter* when removed from the shell is limp and serpentine, the long posterior lobe of the digestive gland occupying half its length. The columellar muscle is a long narrow slip with a deep insertion in the shell and the animal is able to retreat a considerable way. Apart from its small operculum the foot is that of a *Serpulorbis ;* its very prolonged pedal tentacles and the disposition of the head and pallial organs suggest that *V. triqueter* is an accomplished mucous trap feeder (see also Yonge & Ilse, 1939). It approaches closest in this respect to *Serpulorbis gigas*. The pedal tentacles appear, however, even longer than in *gigas*, being extremely slender and tapered, with a ciliated groove running along their mesial sides as far as the tip. They diverge from the median opening of the very

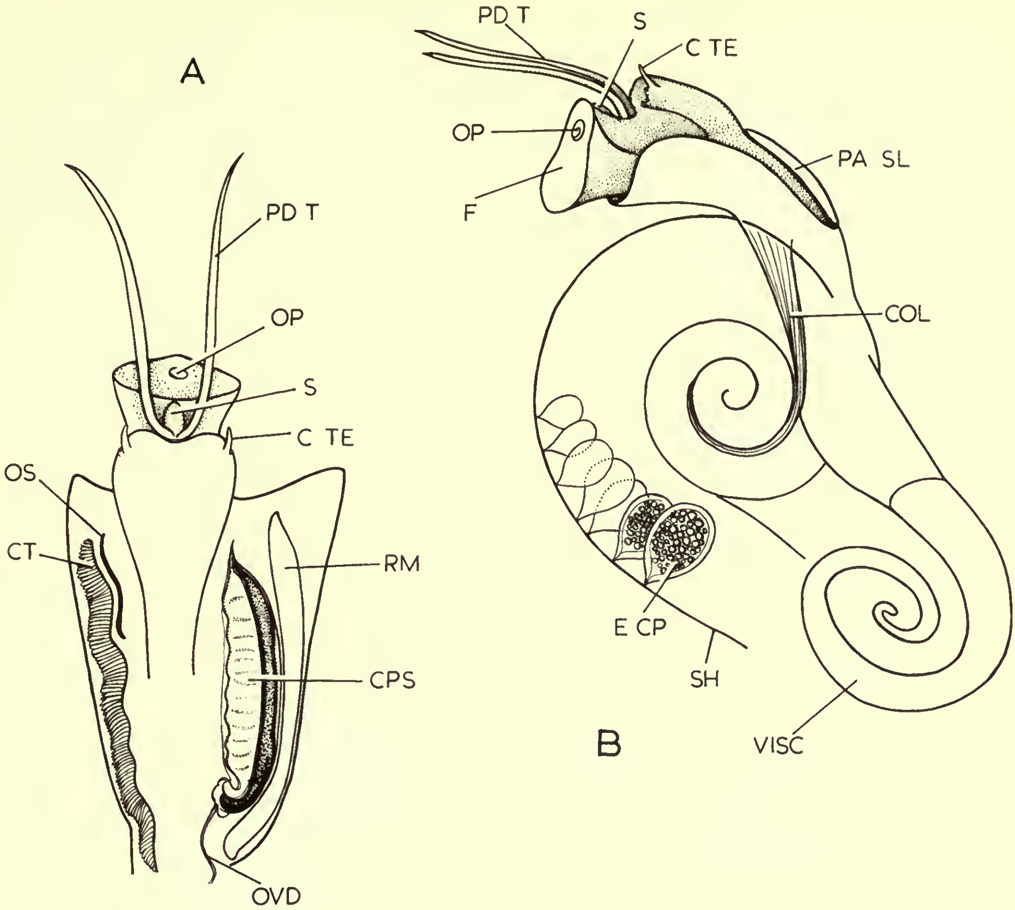
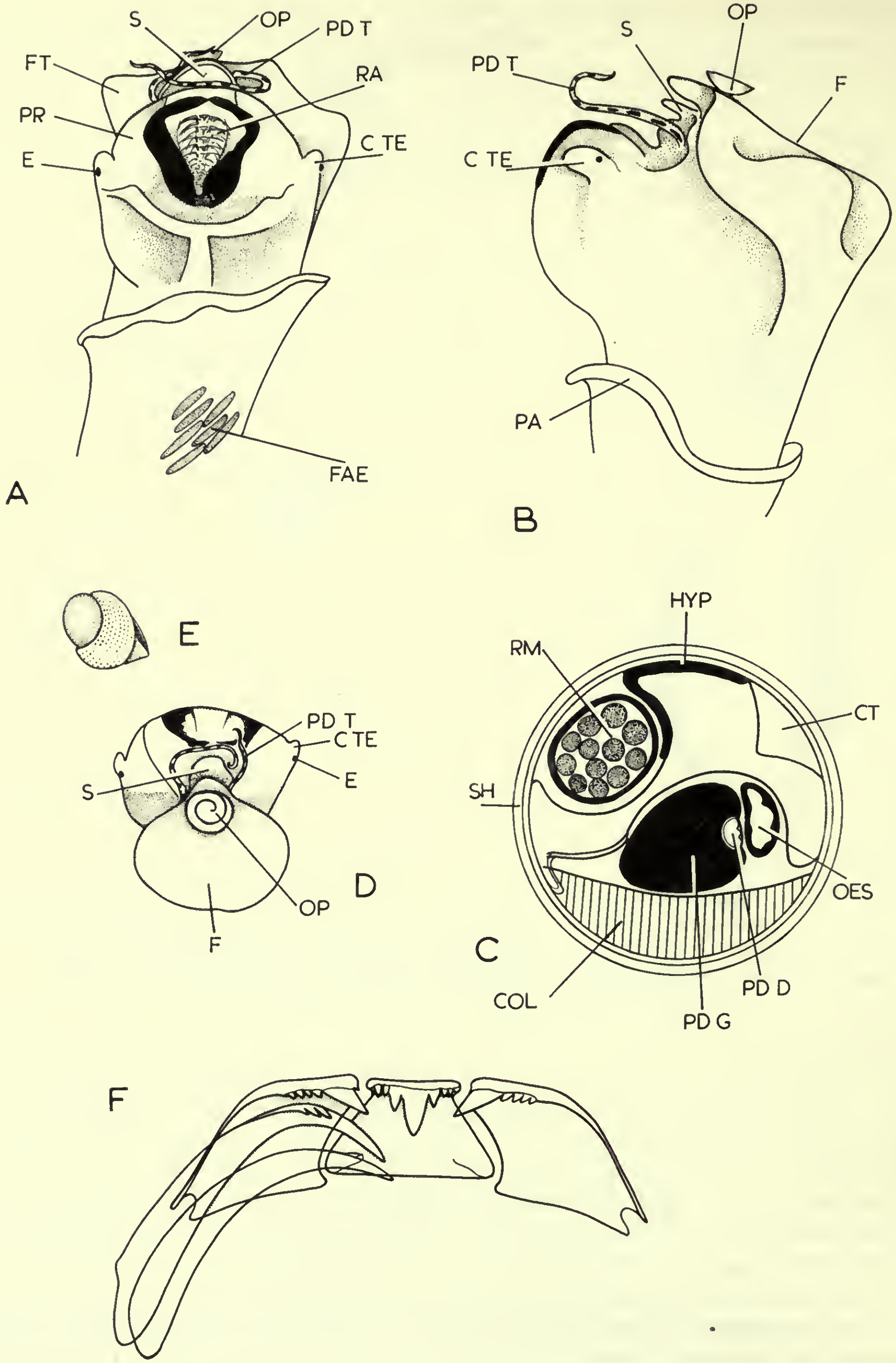


FIG. 11. *Vermetus triqueter*. A. The anterior part of the animal showing the head, foot and pallial cavity of the female after opening the pallial cavity in the dorsal midline. B. Diagrammatic view of the whole animal with the visceral mass slipped out of the shell which is shown in section to illustrate the mode of attachment of the eggs. Both figures are adapted from Lacaze-Duthiers (1860).

large pedal gland, in front of which and between the tentacles is the small ovoid area representing the sole of the foot. The large and bulbous head is crowned with very short cephalic tentacles. The head has no trace of a deepened food groove upon the right side, nor of a flat food tract, such as is found in *Serpulorbis zelandicus*. The possibility of ciliary feeding is further negatived by the exceedingly small dimensions of the gill filaments. Although the gill extends the full length of the mantle cavity, it is as narrow as that of *S. gigas*, and its filaments form tiny equal-sided triangles. The wide area of the hypobranchial gland is left entirely uncovered by the small gill at its left.

V. triqueter displays the same reproductive adaptation as *Serpulorbis* in enclosing the eggs in thin, teardrop-shaped capsules affixed in a single row to the lining of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the shell of the female. The pallial skirt is in the same way deeply incised in the dorsal middle line. The female reproductive tract is extremely similar to that of *Serpulorbis zelandicus* : the capsule gland does not run the length of the mantle cavity, but forms an ovoid purse ventrally slit open, and evidently capable of secreting and affixing a single capsule at one time. Lacaze-Duthiers figures seven capsules and states the egg number in each to be 10–30. The embryo has the conical to globular shell characteristic of *Serpulorbis*, with 1–2 whorls ; the velum is reduced and the liberated embryo settles at once, without any stage of free-swimming.

Vermetus adansonii, as illustrated in Text-figs. 12A–D has a head and foot greatly recalling those of *Serpulorbis*. The head with its contained buccal mass is undoubtedly massive in life, but its great size relatively to the foot may be in part the result of unequal shrinkage of the latter in drying. The foot is naked on the terminal disc except for a small concave saucer-shaped operculum, about one quarter the diameter of the foot after preservation. Though smaller, it is a typical operculum derived from the *Petaloconchus* type with an upstanding spiral flange of 1–2 volutions. The very similar operculum of *V. triqueter* is illustrated in Text-fig. 11. There is no *a priori* reason for expecting the reduction (or total loss) of the operculum to be a monophyletic happening in the Vermetidae ; but there does in fact appear to be a strong affinity between these two species assigned to *Vermetus* s.s. and to all the *Serpulorbis* species examined.

The pedal tentacles of *V. adansonii* are especially long, and are finely tapered and whip-like. A further resemblance to *V. triqueter* is seen in the mantle cavity (Text-fig. 12C) where the gill is of the smallest proportions, with equilaterally triangular filaments, and the pedal gland as revealed in cross section is very large, one of the best developed among all the Vermetidae.

I could examine no female specimen of *V. adansonii*, and thus can report nothing about the condition of the capsule gland, or as to whether the mantle edge is deeply incised as in *V. triqueter*. A single embryo shell obtained is illustrated as Text-fig. 12E and exhibits a strong general resemblance to the conic-globose apex of *Serpulorbis* (see Keen, 1961).

The radulae of several species of *Serpulorbis* and of *Vermetus adansonii* share a strong similarity and are easily distinguishable from radulae of *Dendropoma* or of *Petaloconchus*. The median tooth is not rectangular with the addition of postero-lateral horns, but is roughly trapezoidal, with straight or somewhat convex sloping sides and a long median cusp. The postero-lateral corners are of even thickness with the rest of the tooth and are never built out into horn-like projections. The lateral teeth are not greatly different from those of *Dendropoma*, and the second marginal teeth are smooth of cusps or have a distally-directed spine rather less prominent than that of *Dendropoma*. They lack the four or five denticles of these teeth in *Petaloconchus*.

FIG. 12. *Vermetus adansonii*. A. The head, foot and anterior part of the pallial region in dorsal view. B. The same structures viewed from the right side. C. Diagrammatic transverse section through the pallial cavity. D. The head and foot viewed from above. E. The embryonic shell. F. A single row of teeth of the radula, omitting the marginals on the right side.

3. EVOLUTIONARY TRENDS IN THE VERMETIDAE

With knowledge of a wide enough range of characters, convergent evolution should be no impediment to natural arrangement. Convergence affects characters and seldom whole organisms, and though several characters may often be linked in an adaptive complex (here for example the gill, pedal gland and pedal tentacles concerned in feeding), and there generally remain some features not implicated in adaptation, and forming signposts to the lines of natural cleavage. The organism is a mosaic of characters evolving at different rates, and there is not one character which—studied alone—may not be misleading in classification. And insofar as the recognition of lines of descent is a respectable object of study, it is—like the delimitation of species—a product of the judgment of the investigator ; there seems no formula by which the evolutionary importance of particular characters, or of degree of progress in different trends, can be made the objects of measurement. The phenotypic extent of a particular character may have no necessary correspondence with length of evolutionary time, or phylogenetic separation.

To discuss the evolution of a homogeneous family such as the Vermetidae, one must consider the *evolutionary trends* running through the group : a number of these will be separately recognizable, usually proceeding without detailed correspondence with each other. Trends are characterized by direction ; and to recognize the primitive condition and direction of advance is again a matter of judgment. With hard parts one could look ideally at the fossil record, but this is frequently lacking and always so with soft tissues. Several rules may, however, be followed, whether by analogy with other prosobranch groups, or from correlation of structure with known function in the Vermetidae itself. Evolution proceeds from the general to the novel, from structures widely possessed to structures specially adapted. For example, gill filaments narrow and linear may reasonably be derived from broad triangular ones characteristic of prosobranchs as a whole. The mantle slit of the female *Serpulorbis* is an advanced feature as compared with the lack of it. A multispiral apex is generally held to have given rise to a paucispiral one and not the reverse (see Finlay, 1931 ; Thorson, 1950), and is in turn to be correlated with a change from free-swimming veligers to retained young. Both the high elaboration and the loss of the operculum may be regarded as conditions subsequent to the possession of a normal sized unelaborated operculum.

Table 1 sums up the evolutionary trends that will be considered in the following discussion. The presumed primitive condition is set out in the central column, and the columns to left and right show the one or more derived conditions represented in various parts of the family. The content of the " derived " columns of the left and right will be found—on reference to the schematic diagram on the opposite page—to be selected according to the views advanced in this paper as to the derived condition of *Dendropoma* and *Serpulorbis* with respect to the more " central " genera within the Vermetidae. The shading conventions, whether black or vertical or cross-hatched are chosen to represent differently specialized conditions of each character, corresponding to different genera.

(i) THE APEX

The young vermetid just before settlement is closer in form than it will ever be afterwards to more normal gastropods. As Dr. Keen has shown, the first vermetid peculiarity appears at the time of attachment when the helicoid embryo shell settles upon its side and the direction of coiling is changed, as the first post-embryonic whorls become attached to the substrate. Such a movement of the axis of volution through 90° is the salient distinguishing feature of the apex of a true vermetid. The apex would seem, moreover, to provide one of the most reliable taxonomic characters at generic and specific level, yet even this is not wholly free from adaptive involvements. Finlay (1931), Thorson (1950) and others have shown the correlation for prosobranchs in general of a smaller multispiral apex with smaller sized eggs and free-swimming veligers, and of a larger paucispiral apex with larger eggs and the suppression of free-swimming. In the Vermetidae we find apices with the largest number of whorls (3–4) in *Petaloconchus*. *Serpulorbis* has usually two to three whorls and the larger apex of *Dendropoma* has typically one-and-a-half whorls. Finlay has postulated that the reduced paucispiral apex never gives rise to the multispiral but that evolution in the other direction frequently occurs. We know accurately the life history of very few vermetids. For *Serpulorbis aotearoicus*, I have shown conclusively (Morton, 1951a) that there is no free-swimming stage and that the actively crawling embryo attaches very shortly after emergence from the maternal shell (see Text-fig. 8G). The eggs are few (c. 10) and large. We may clearly infer the same condition for *Vermetus triqueter*, and so far as we can tell this appears to be the more general vermetid rule. There is a relative lack of any records of known vermetid larvae from the plankton (see, however, Lebour, 1945). We have, however, the interesting case of *Serpulorbis imbricata* which releases free-swimming larvae with well-developed four-lobed vela. The eggs here are very much smaller and more numerous than in *S. aotearoicus*, lying in a row of 20–30 attached capsules, each with some 70 or 80 eggs of which some are devoured as nurse eggs by other embryos. The apex of *S. imbricatus* is long-spired for a *Serpulorbis*, with three-and-a-half whorls at settlement. *S. aotearoicus* settles with only two whorls. Its velum, though small and not divided into lobes, is still prominent, with its cilia beating while still within the embryonic capsule ; larval retention is evidently a phylogenetically recent development in this genus. *Vermetus triqueter* exhibits retained veligers at much the same level of development. If we may take the number of apical whorls as a provisional index to the type of life history, we would expect in *Dendropoma*—a derived group with a large paucispiral apex—to find no free-swimmers. The New Zealand *D.* (*Novastoa*) *lamellosum* certainly hatches crawling embryos direct (Morton, 1951a). *Petaloconchus* has a small rather cylindrical apex, regularly of three to four whorls ; *Serpulorbis* has a rather more conical to ovoid apex, with the whorl number two to three and subject to reduction. From the apex of *Petaloconchus* we should be tempted to look in this genus for species with free-swimming veligers[1]; the oldest embryos retained in the mantle cavity

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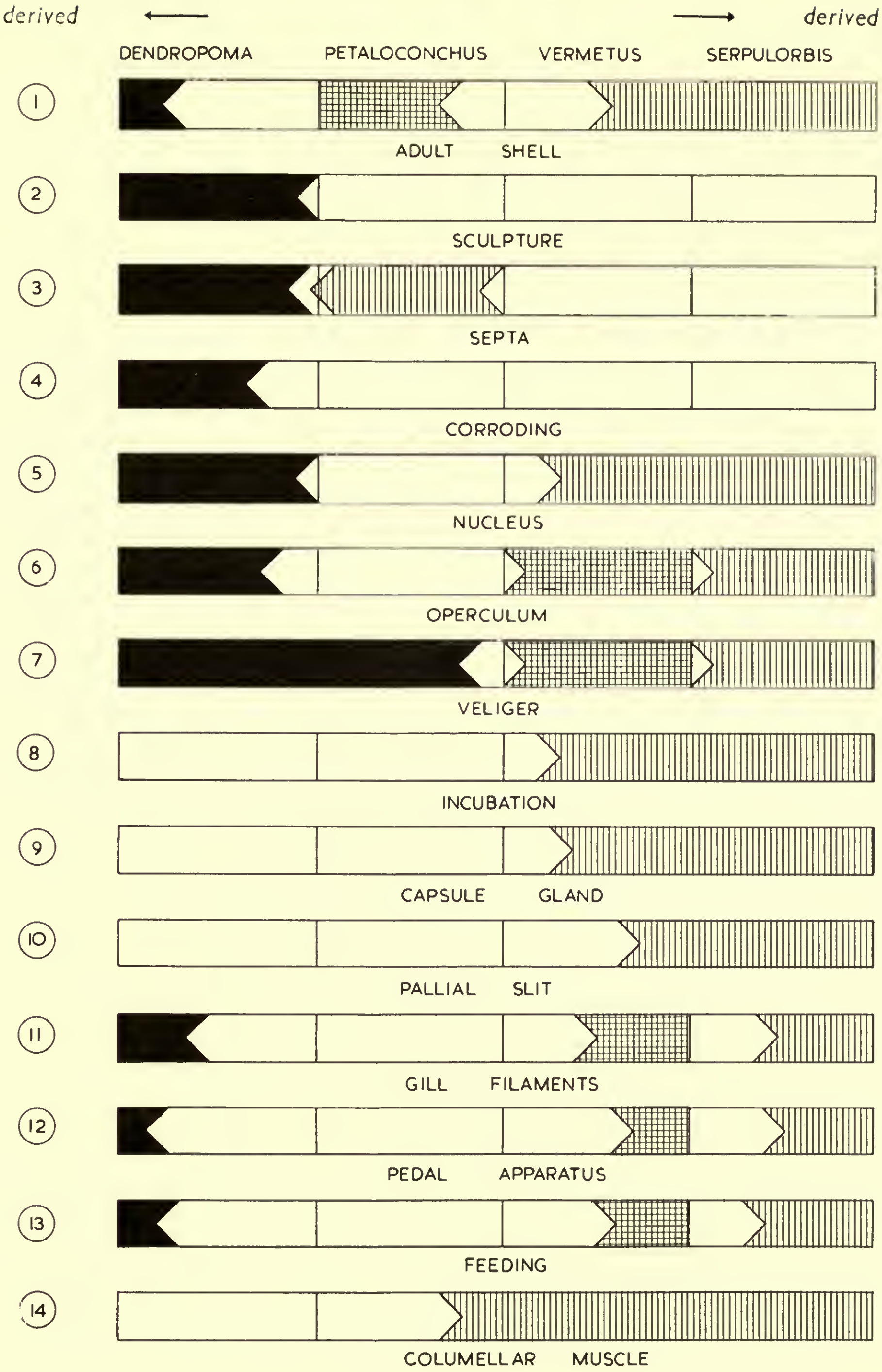
[1] Since this was written, Robertson (*in litteris*) advises me that he has observed the free-swimming veligers of *Petaloconchus nigricans* at Bimini, Bahamas.

TABLE 1. EVOLUTIONARY TRENDS

Derived		*Primitive*	*Derived*
Adult shell a straight upright tube	1	Adult shell an open, sometimes irregular spiral of several turns	
Sinous growth lines predominate, often with sharp ridges or toothed keel	2	Sculpture both transverse and longitudinal, often cancellated	
Shell with internal transverse septa	3	Shell lacking internal subdivision	Shell with internal longitudinal lamellae
Shell corroding the substratum	4	Shell applied to surface of substratum	
Nucleus reduced to 1–2 whorls	5	Nucleus small and multispiral, of 4–5 whorls	
Operculum with an axial mamilla and variously enlarged and strengthened	6	Operculum a thin saucer, sometimes with a spiral flange	Operculum reduced to a button or lost in adult
Free-swimming stage lost, eggs larger and few	7	Numerous small egg and free-swimming veligers	
	8	Egg capsules lie freely in the mantle cavity	Egg capsules attached to inside of shell
	9	Capsule gland a long furrow	Capsule gland short and purse-like
	10	Mantle of female entire	Mantle of female with median incision
Gill filaments narrow and tending to elongate	11	Gill filaments large and triangular	Gill filaments triangular but reduced in size
Gland and tentacles reduced	12	Pedal gland large and tentacles moderately long	Gland and tentacles very large
Ciliary feeding predominates	13	Mixed ciliary and mucous feeding	Mucous feeding predominates
	14	Columellar muscle short and inserted far forward	Columellar muscle a long strap deeply inserted


derived
derived
DENDROPOMA
PETALOCONCHUS
VERMETUS
SERPULORBIS
①
ADULT SHELL
②
SCULPTURE
③
SEPTA
④
CORRODING
⑤
NUCLEUS
⑥
OPERCULUM
⑦
VELIGER
⑧
INCUBATION
⑨
CAPSULE GLAND
⑩
PALLIAL SLIT
⑪
GILL FILAMENTS
⑫
PEDAL APPARATUS
⑬
FEEDING
⑭
COLUMELLAR MUSCLE

of *P. montereyensis* had only two to two-and-a-half whorls, suggesting a further pre-settlement period, possible free-swimming, before the growth of the embryo shell is completed. In *Serpulorbis* free-swimming is to be suspected in those species with more whorls (as in *imbricata*) and the free-swimming habit was perhaps abandoned in other *Serpulorbis* species more recently than in *Dendropoma*. The greatest gap in our knowledge is of the life history of *Petaloconchus :* fortunately there are several American species from which this may be remedied.

(ii) THE ADULT SHELL

The disposition and coiling of the post-embryonic and adult tube is—as Dr. Keen has shown—of a characteristic type for each of the vermetid genera. This pattern is seldom likely to have adaptive significance, although the straight upturned terminal part of the tube is probably so disposed as to assist the putting out of mucous traps with the minimum of impediment from the substratum or from adjacent tubes. It is not easy to discern evolutionary trends in coiling pattern : each type, as for example the Greek key of *Dendropoma* or the Turritella pushed sideways of *Petaloconchus*, may be regarded as something *sui generis* and distinctive to its particular group. It is doubtful too whether the colonial habit and massive crowding of tubes is of any phylogenetic value. This occurs in some species of both *Petaloconchus* and *Dendropoma* (in the latter Dr. Keen has suggested it as a character in the recognition of the subgenus *Novastoa*). The larger tubes of *Serpulorbis* tend more often to be solitary or more loosely clustered ; but crowded aggregates may be found as, for example, in *S. squamigerus* where this habit is associated with the communal mess table contributed by the pedal glands of many individuals.

Certain other features of the shell in *Dendropoma* may, however, be regarded as specialised and advanced. The corroding habit is very characteristic and is exclusive to this genus ; so too is the tendency to a greater or lesser degree to straighten up the adult shell into a long cylinder as in *D. maximum*. Further, we find in *Dendropoma* the most specialised sculptural characters : the emphasis of transverse ribbing with sharp upstanding incremental growth lines, to the exclusion of longitudinal sculpture, and the frequent development of spines or beaked projections, well seen, for example, in *D.* (*Novastoa*) *lamellosa* (Text-fig. 3A). In the remaining genera both transverse and longitudinal sculpture is very generally retained, equally and moderately developed, with a tendency towards cancellation.

Internal septation of the shell is most frequent in *Dendropoma*. The early parts of the tube become cut off by apertually concave septa, associated with the shortening of the visceral mass, often seen in *Novastoa* and particularly characteristic of *D. maximum*, so that the animal is plump and finger-shaped, no longer occupying the earlier convolutions of the tube. This in turn may be correlated with the large operculum which cannot be withdrawn into the shell and prevents deep retreat into the disused earlier portions. Another type of closing off of the earlier shell is practised in *Petaloconchus*, which lays down two longitudinal lamellae dividing the earlier tube into two passages communicating by a narrow slit. Only one of these appears to be occupied by the " tail " of the animal which carries (see Text-fig. 6A) a long narrow extension into which the gonad may extend beyond the tip of the digestive gland.

(iii) THE OPERCULUM

The earliest operculum of the vermetid embryo is a circular, flat or shallowly concave, chitinous plate covering and overlapping the back of the foot. It is illustrated for *Serpulorbis aotearoicus* in Text-fig. 8J, and for *Dendropoma irregulare* in Text-fig. 4B. In those adults that possess it the operculum is also circular, and in *Petaloconchus* extends slightly, in *Dendropoma* considerably, beyond the edges of the foot. In *Vermetus* s.s. the operculum is reduced to a tiny button, towards the centre of the foot and in *Serpulorbis* it is wholly lost. In the re-organised adult foot the upward-facing disc that bears the operculum is not, of course, the sole, but corresponds to the back of the metapodium ; the true sole is reduced to a narrow triangular area, squeezed up in the middle line between the terminal disc and the proboscis. It is flanked by the two pedal tentacles, between which, and in front of the sole, opens the duct from the pedal gland. In adult *Petaloconchus* the operculum remains thin and fragile, forming a transparent saucer, not too greatly overlapping for the foot to be withdrawn deeply into the tube. Its line of spiral coiling is raised into a sharp, upstanding spiral flange. The reduced operculum of *Vermetus* s.s. is of the same type which appears to be the earliest and simplest found in a vermetid adult.

In *Dendropoma* the operculum usually becomes highly elaborated and is always large, overlapping the foot and sealing the aperture to such an extent that the animal can retreat only slightly or not at all into the tube. Mörch's valid generic name is descriptively inappropriate ; the animal is quite innocent of any branching structure on the operculum. (Could the author have taken for a *lituellus* operculum that of a *Stephopoma* species having multifid opercular setae? Or were the opercula of his specimens bedecked, as occasionally happens, with calcareous algae?) The dendropomatid operculum may be massively thickened, sometimes built up into a solid dome and often calcified. The earliest species show affinities with the opercula of *Petaloconchus*, as in *D. senegalense*, where the operculum still carries a spiral flange, but is deeply concave, inserted into the foot by a broad conical base. This is strengthened by the development of a dense axial mamilla, projecting upwards as a rounded boss in the exposed concavity. *D. megamastum* shows a similar operculum without, however, the spiral flange and *D. maximum* has the same concave bowl, but with neither spiral flange nor mamilla, or the latter very small. On the other hand, *D.* (*Novastoa*) *lamellosum* has the mamilla greatly enlarged to form an axial pillar with its rounded tip deeply inserted into the foot below, and its exposed end bluntly truncate. A further group of *Dendropoma* species, especially some of those colonial forms of smaller size, have the operculum convexly built up on top by the thickening of its own substance. In *D. irregulare, D. tholia*, and *D. ghanaense*, it forms a convex dome with the axial pillar running through it. (See Text-fig. 15 for range of opercular structure in *Dendropoma*.)

The reduction and loss of the operculum in *Vermetus* s.s. and *Serpulorbis* is clearly a derived condition ; so is its elaboration in *Dendropoma*, with the domed opercula of *corrodens, tholia* and *corallinaceum* evidently most advanced. It is suggested that the primitive adult operculum is most closely approached by species of *Petaloconchus*, where the spiral flange—though possibly not primitive—has been found in all representatives studied. The embryonic operculum is an even simpler concave plate.

(iv) CILIARY AND MUCOUS FEEDING AND RELATED ADAPTATIONS

In the following species only is the mode of feeding known from direct observations of the living animal :—

Species	*Feeding*	*Authority*
Serpulorbis gigas	Entirely mucous	Boettger, 1930
Serpulorbis aotearoicus and *S. zelandicus*	Mixed ciliary and mucous	Morton, 1951a
Serpulorbis squamigerus	Entirely mucous with a communal mess-table	MacGinitie & MacGinitie, 1948
Petaloconchus nigricans	Chiefly mucous with a smaller amount of ciliary	Robertson (1959), (*in litt.*)
Serpulorbis sp.	Mucous ; ciliary not observed	Keen (1959), (*in litt.*)
Dendropoma maximum	Entirely ciliary	Yonge, 1932
Dendropoma lamellosa	Chiefly ciliary, with a smaller amount of mucous	Morton, 1951a
Dendropoma irregulare	Mixed mucous and ciliary	Robertson (1959), (*in litt.*)

In *Serpulorbis gigas*, and *Serpulorbis squamigerus* (and also probably in *Vermetus triqueter*) on the one hand, and in *Dendropoma maximum* on the other, there is thus reported to be exclusive reliance on one feeding method with the abandonment of the other. The other species studied grade between these two extremes. In vermetids not yet investigated in life, the methods of feeding available are often a matter of reasonable inference from the anatomy : there are fortunately a number of structural characters that appear to be correlated with the predominance of one method or the other, though care should be taken not to exclude either method even upon what appear to be reasonable anatomical grounds.

Every known vermetid possesses a well-marked pedal mucous gland extending into the haemocoele alongside the oesophagus and opening in front of the foot between the two pedal tentacles. Yonge and Iles (1939) have well described its two extremes of development in *Serpulorbis gigas* and *Dendropoma maximum*. The homologies of the pedal gland are uncertain. In certain Rissoacea there is also an important pedal mucous gland of such a size as to have become haemocoelic in position ; Graham & Fretter regard this as a highly developed ventral pedal gland from the position of its opening upon the surface of the sole. In the Vermetidae, so far as the morphology of the vestigial foot can be regarded as clear, the mucous gland would appear to open at the anterior edge of the foot upon what corresponds to the metapodium, and its closest resemblances to be with the anterior pedal gland, generally and to a varying extent developed in prosobranchs. The Vermetidae have no very close known relatives to which we might turn for any clue as to the original or intermediate condition of their mucous gland. Equally strikingly, it is present well-developed in every vermetid examined.

The homogeneity of this structure within the family, and the evidence of feeding habits within each of the four genera make it overwhelmingly likely that the gland was at its first appearance developed as a means of food-collecting. Contrary to the tentative view I have previously expressed (Morton, 1955), there seems every likelihood that mucous trap feeding was an early and probably an original activity of the Vermetidae. Of all mesogastropod families that are able to practise ciliary feeding, the Vermetidae have undergone the least specialization in the filaments of the gill or the other food collecting structures of the mantle cavity : ciliary feeding is a condition to which—as a family—they have never become deeply committed. With the exception of *Dendropoma maximum* it is probably the exclusive habit of rather rather few species. Nearly all vermetids probably make use of both methods of feeding.

Nevertheless, the most extreme development of mucous feeding, with the greatest enlargement of the mucous gland and—in particular—the elongation of the pedal tentacles and the reduction in extent of the gill are evidently a later feature confined to *Vermetus* s.s. and *Serpulorbis*. Even in species where this would seem anatomically unlikely, particles are collected within the mantle cavity and carried forward on the right side to the neighbourhood of the mouth in a food groove or open tract of varying elaborateness.

The retention of an operculum spreading widely beyond the margin of the foot, and the small or even rudimentary condition of the pedal tentacles, cannot have favoured development of mucous feeding, and where we find this condition, as in *Petaloconchus* and particularly in *Dendropoma*, an admixture of ciliary with mucous feeding has generally been shown to occur. More evidence on the feeding habits of species of *Petaloconchus* will be eagerly awaited, in particular the publication of Robertson's full report. The pedal gland of both *P. montereyensis* and also of *V.* (*Thylaeodus*) *contortus*, though narrow, is very large as a result of the great prolongation of the pallial region. Here the operculum overlaps the foot only relatively slightly ; and in *P. nigricans*, reported by Robertson to feed by mucous traps, there is no overlap at all. There would appear to be little in the anatomy of the genus *Petaloconchus* to disable its members from either type of feeding. The provisional view may be taken that the original feeding habit of the Vermetidae included resort to both mucous and ciliary means, and that the genus *Petaloconchus* most nearly represents this condition. In their feeding organs, as in much of the rest of their anatomy, the two species of *Vermetus* s.s. examined come very close to *Serpulorbis* and cannot be considered unspecialized. At the other extreme, the genus *Dendropoma* has in many of its species retained a primitive ability to collect food by ciliary means, and has in at least one species developed this method exclusively.

It has often been suggested, as by Yonge and Iles (1939), and in my own papers on New Zealand vermetids, that there is an ecological correlation with the mode of feeding. Without more knowledge of the distribution of feeding habits within the family, it is difficult to generalise. In exposed situations with continually broken waters and wave disturbance, mucous traps might be difficult to put out or to maintain successfully and ciliary feeding might be expected to be best developed. The outstanding example is *Dendropoma maximum*, living on the surf-beaten outer ramparts of the Great Barrier Reef. In general it may be said of *Dendropoma* that the typical ecological form is that of small to medium-sized vermetids, frequently colonial and zone-forming on the exposed surfaces of open shores, and often deeply impacted in coralline algae or eroding the substrate during their growth. *D.* (*Novastoa*) *lamellosa* in New Zealand is an intertidal animal diagnostic of exposed off-shore islands with considerable wave attack. *D. irregulare* in the West Indies would appear to be an inhabitant of coralline-encrusted, very wave-exposed rocks. On the other hand, these two species, like *Petaloconchus nigricans*, also occurring in rough water, are able to practise varying amounts of mucous feeding.

In *Serpulorbis* and *Vermetus* s.s. on the other hand, we may recognise a general preference for quieter and more sheltered situations, though there are numerous exceptions. These vermetids are frequently solitary or semi-solitary, grow to a larger size, with the shells often emergent above the substratum, never corroding and seldom becoming encrusted. They are frequently found beneath rocks or protected by ledges where mucous traps could best be employed without disturbance, extending freely into still water until hauled in. The under-stones or sheltered habitat is so far as I know unrecorded for species of *Dendropoma*.

Reduction and loss of the operculum is correlated in *Serpulorbis* and *Vermetus* s.s. with a greater perfection of mucous feeding. Whether the condition of the operculum has had a " pre-adaptive " influence in determining the mode or predominance of feeding, it is difficult to determine. These different adaptive trends are obviously interwoven, but to discern any simple cause and effect relation between them may be to oversimplify.

But the condition of the operculum carries in its train other adaptive implications. Thus, in *Dendropoma*—with an operculum as wide as the shell tube—the animal cannot retreat for long distances into the tube, although its quickness of response in darting back and closing the tube with the operculum is very striking. In *Petaloconchus* with the operculum not quite so wide as the tube, and in *Vermetus* and *Serpulorbis* with it reduced or lacking, the animal on disturbance retreats deeply into the earlier reaches of the tube and with the loss of the operculum this is the chief protection from attack. *Dendropoma* will then retain a more or less constant position of the animal in the distal and later formed part of the tube. The columellar muscle is a short and thick strap forming the structural support of the pallial region as it runs forward to become continuous with the foot. It attaches somewhat distally to the tube at the level of the anterior half of the body. In *Petaloconchus* and *Serpulorbis* the columellar muscle is more slender, plays less part in the structural support of the pallial region of the body, and becomes drawn out into a narrow strip that extends far backwards into the tube alongside and independent of the rest of the body. Its posterior insertion marks the deepest point towards which the anterior half of the body can be drawn back, with the visceral mass sliding freely behind it.

This reaction takes place in a flash when the animal is disturbed and disappears beyond sight into the earlier coils of the shell. In correlation with the lesser use made of the deeper parts of the tube, we find the tendency in many species of *Dendropoma* to cut off the earlier parts of the tube by aperturally concave septa. In this way the body of the animal may become considerably foreshortened. Compare, for example, the finger-shaped body of *D. maximum* with the limp, vermiform visceral mass in most *Serpulorbis*, or the many-coiled, slenderly elongate animal of *Petaloconchus*. In some specimens of most *Dendropoma* species, the visceral mass is truncate and foreshortened, in other specimens the full visceral spiral will be found. This tendency seems to have proceeded furthest in *D. maximum*, where the animal is hardly if at all curved, and lies entirely in the straight terminal part of the tube. The formation of shell septa is unusual in *Serpulorbis*, being not mentioned as a diagnostic character by Keen (1961), though I have found aperturally concave septa in *Serpulorbis zelandicus* (see Morton, 1951a, page 4).

Deep retreat into the tube has its effects in turn on the mode of protection of the eggs, which in this family can take place in one of two main ways. First, in *Dendropoma* and *Petaloconchus* up to a dozen egg clusters lie freely in the mantle cavity of the female, in a single row reaching from near the mantle edge to the top of the mantle cavity, beneath or to the right of the rectum, on the side away from the gill. In *Vermetus* s.s. (at least in *V. triqueter*) and in all species of *Serpulorbis* I have seen, the egg capsules are contained in a row of teardrop-shaped capsules attached by short stalks to the inner surface of the shell of the female. These lie in a median row of a dozen or fewer, reaching nearly to the aperture of the tube. The mantle of the female is deeply incised to allow the egg capsules, while remaining fixed to the shell, to lie within the mantle cavity of the expanded animal. On retreat the animal leaves the attached eggs unguarded near the shell aperture and darts back without them. Eggs retained fully in the mantle cavity as in *Dendropoma* would be crushed or damaged on retreat by the retraction into the mantle space of the foreshortened and thickened head and foot. There would be no room for both. In *Serpulorbis* the foot is softer and more flexible than the muscular plug of *Dendropoma* and can be contracted away from the egg capsules as it passes them on going down into the shell. In *Petaloconchus* deep retreat is still, however, possible with eggs lying freely in the mantle cavity and carried back with the animal. Here—as will be seen from Text-fig. 6A, B—the mantle cavity is usually much longer than in *Serpulorbis* and the egg capsules are not individually so bulky, each appearing to contain a single embryo only. The head too seems to have a smaller bulk and to lie flatter against the contour of the foot than in *Serpulorbis*. It must on retreat present less obstruction to the eggs which—as in *M. montereyensis*—lie to one side of it, on the right of the mantle cavity. The prominent bulge of the head in *Serpulorbis*—it may be almost as large as the foot—is (as has been mentioned) due to the enlargement of the buccal mass, which in mucous trap feeders serves not only to rake in food boluses but in addition to haul downwards the bulky mucous traps before ingesting them.

(v) REPRODUCTIVE SYSTEM

A thorough examination of the structure and action of the genital ducts in female vermetids is much needed ; only the short account for *Serpulorbis* by Morton (1951a) has given this system more than glancing mention. Like other attached and non-motile prosobranchs (except the Calyptraeidae) the Vermetidae are aphallic. Gregarious habits will ensure that sperm released into the water by the male is carried into the mantle cavity of the female in her inhalant current ; and the pallial genital duct of the female consists of a glandular tube widely slit open down one side to receive the sperm (see Fretter (1946) on *Turritella*). The ovary leads into a narrow prominal ovarian duct carrying the ova to a small spherical albumen gland lying at the posterior end of the mantle cavity on the right side. This opens into the much longer, ventrally open capusle gland. At the junction of these two glands, open one or more tiny rounded pouches, forming together a receptaculum seminis where incoming sperm lie oriented by their heads to the lining epithelium.

In *Dendropoma*, see for example *D. maximum*, the capsule gland is a very long furrow, lined with a thick secreting wall on either side and open in the ventral line. It extends forward along the mantle wall ventrally to the rectum and reaches as far as the anus. It secretes the thin horny capsules round the long row of eggs or egg clusters that first lie within it, and are then turned out to remain freely within the right side of the mantle cavity until the crawling shelled embryos emerge. The female of *Petaloconchus* has a similar genital duct. (See Text-fig. 6B, C).

In *Serpulorbis* on the other hand, the capsule gland is a short semicircular pouch open along its straight side, and much more confined to the posterior part of the mantle cavity. It is situated just behind and to the right of the median pallial incision. A single egg capsule at a time is elaborated in it and completely fills its lumen. These capsules are one by one attached to the lining of the shell, the oldest lying in front. The ventral opening of the capsule gland can by means of the pallial incision be brought into direct contact with the lining of the shell as the egg capsules are extended.

(vi) THE RADULA

Where uniformity of diet within a family can be known or reasonably assumed, the radula is often found to provide detailed taxonomic differences apparently unrelated to differences in habit. Sometimes, as for example in the ciliary feeding mesogastropod family Struthiolariidae, the diagnostic differences in the cusp pattern of the reduced radula must have been developed well below the minimum size level of adaptive play (Morton, 1956b). In the Vermetidae, though the radula is short and " S "-shaped, with the upturned tip of its sac hidden beneath the buccal mass, the teeth are still somewhat robust. As in most ciliary feeding gastropods, the erectile laterals and marginals serve to seize boluses of mucus-bound food. In mucous trap feeders especially the paired, sharp-edged lateral jaws play an active role in grasping the food bolus ; a medium-sized *Serpulorbis* will firmly seize and hold a needle tip placed between the jaws.

The radula is a conservative structure within the family Vermetidae, and is in the first place useful in confirming the homogeneity of the family as a unit to the exclusion of *Stephopoma*, *Siliquaria* and *Vermicularia*. The main subdivision within the family is indicated by the shape of the central tooth. In the first group consisting of the operculate genera *Dendropoma* and *Petaloconchus*, the base of the central tooth is a squarish to rectangular transverse plate, with its posterior corners drawn out into very distinct curved or peg-like projecting horns. In the second group, consisting of the genera *Vermetus* s.s. and *Serpulorbis*, this central plate is distinctly trapezoidal in shape, a good deal wider across the posterior than the anterior edge, and its posterior corners are provided with prominent horns. The

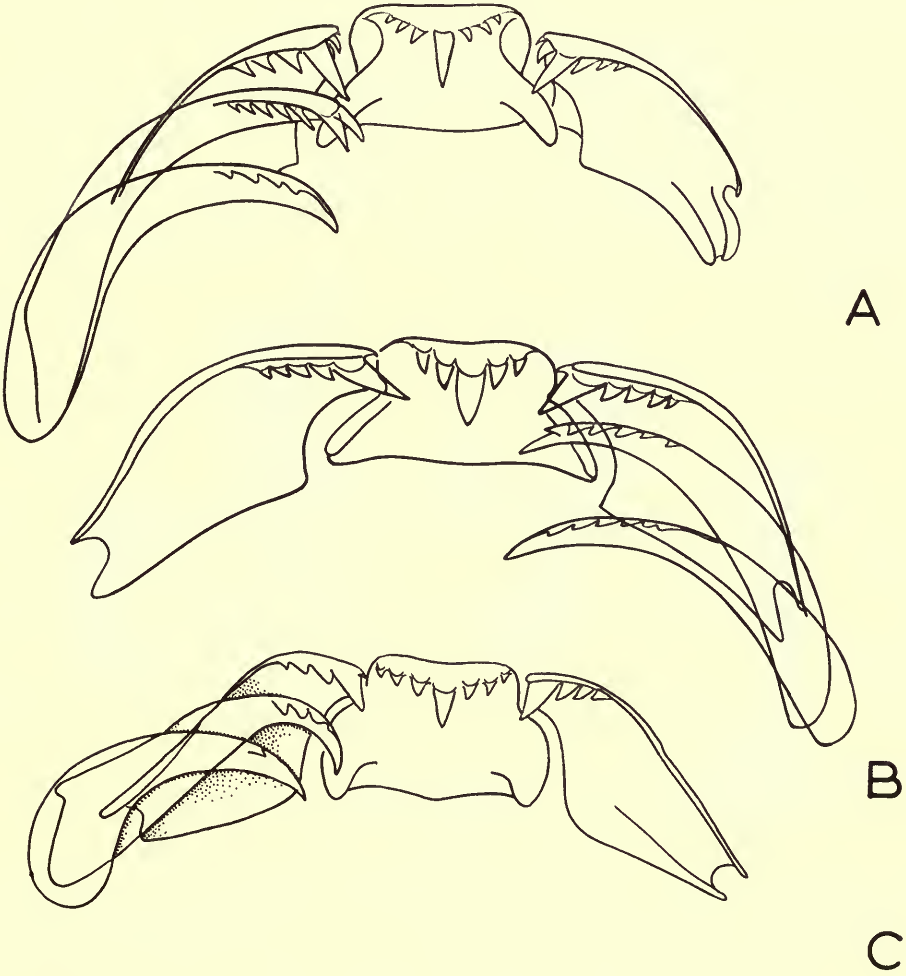


Fig. 13. Single rows of teeth from the radula of selected species of Vermetidae. The marginal teeth are variously omitted from one or other side. A. *Vermetus* (*Thylaeodus*) *contortus*. B. *Petaloconchus montereyensis*. C. *Dendropoma corallinaceum*.

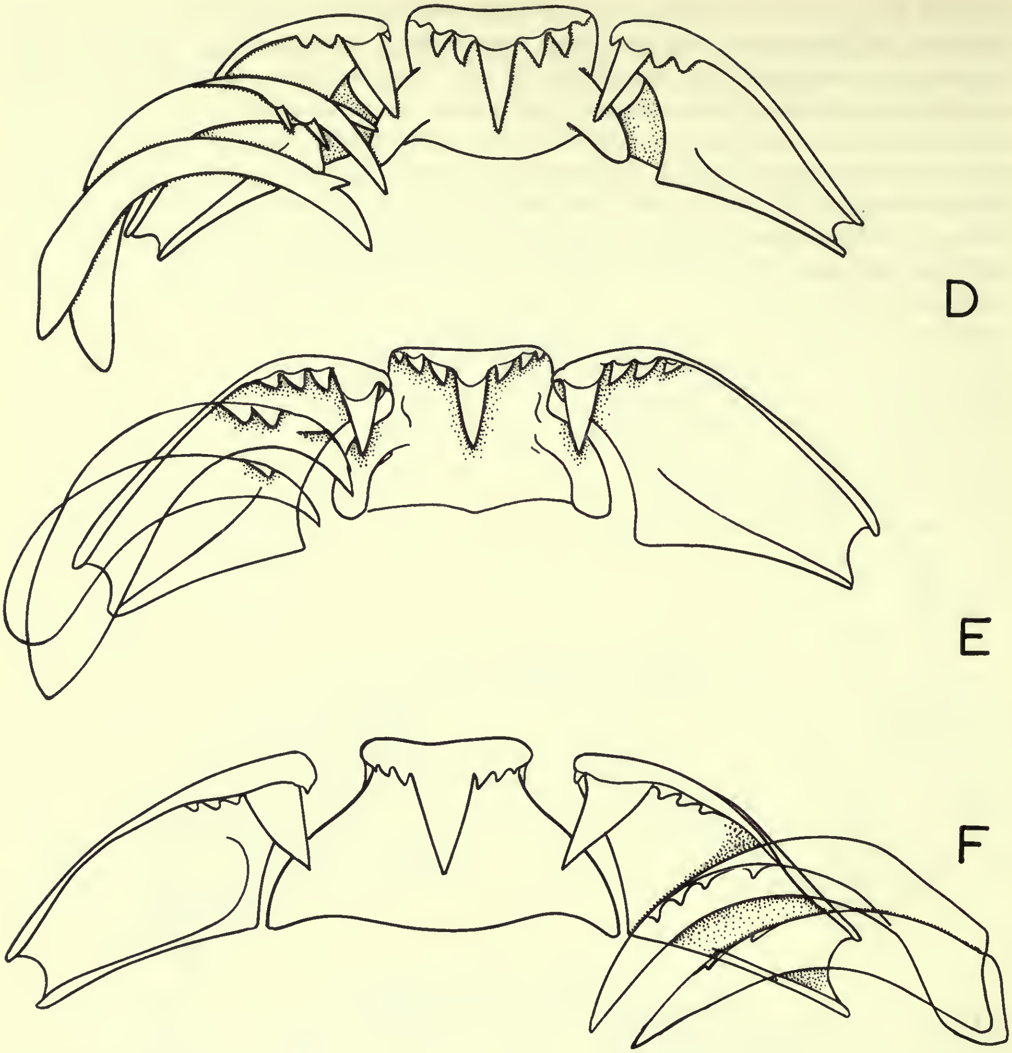


Fig 13 (*continued*)
D. *Dendropoma ghanaense*. E. *Dendropoma tholia*. F. *Serpulorbis zelandicus*.
(Compare also with *Vermetus adansonii*, Text-fig. 12F)

marginal teeth provide a further distinction between *Dendropoma* and such species as *Petaloconchus* as I have been able to examine. In *Dendropoma*, the first marginal bears just behind the tip a group of usually two sharp serrations on either side, distally to which is a spine-like apically-directed denticle. The second marginal bears this denticle alone, lacking other serrations. In the first marginal of *Petaloconchus* the serrations are five in number on either side of the tooth, with the spine-like denticle again directed apically. The second marginal has no spine-like denticle, only a line of five very reduced serrations at either edge. In *Serpulorbis* the first marginal bears two or three serrations at either edge, and the second marginal a reduced spine-like denticle alone. (See Text-figs. 13A–F for generically typically radulae.)

(vii) PHYLOGENY

The facts now established about the animals of 20 species of the Vermetidae, and such insight as we have gained into the relation of structure to habits, invite some consideration of the possible lines of descent and relationships of the vermetid genera. In my shorter review of vermetid adaptations (Morton, 1955), after severing the Siliquariidae and *Vermicularia* from the Vermetidae, I proposed a dichotomy of the family into two lines, the one characterized by predominantly ciliary feeding and retaining the operculum (the "genera" now grouped in *Dendropoma* and *Petaloconchus*), and the other comprising chiefly mucous feeders with reduction or loss of the operculum (now *Vermetus* s.s. and *Serpulorbis*). While such a division still broadly holds good, certain of my previous conclusions require modification, after access to a wider range of species. First, I can no longer advocate the basically primitive position assigned to "*Vermetus novae-hollandiae*" (= *Dendropoma*

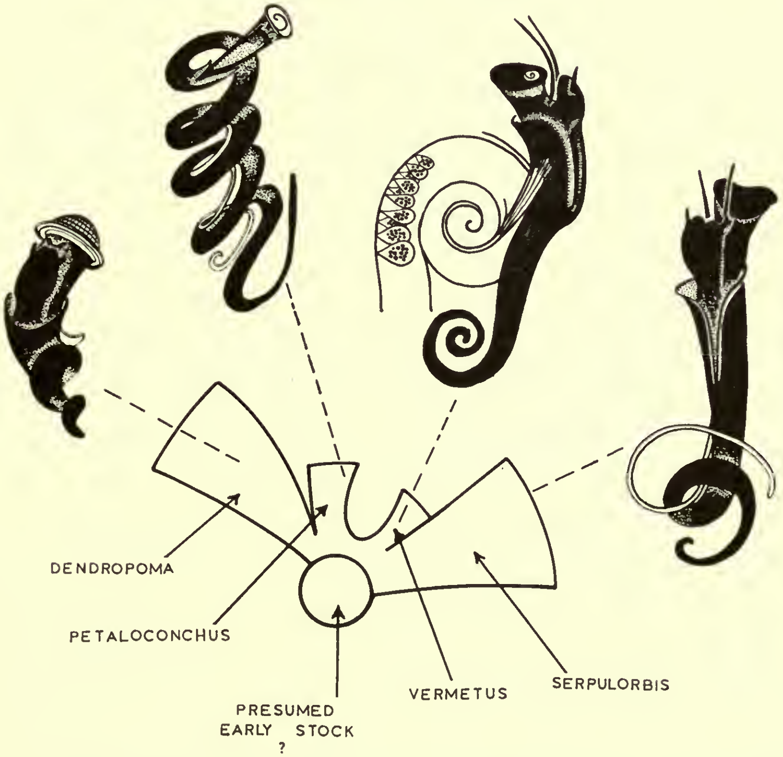


Fig. 14. A diagram of the evolutionary radiation of the genera of the Vermetidae as suggested in the accompanying discussion.

maximum), on the basis of its feeding habits and operculum. This species has proved in many ways a misleading example of its genus, giving little indication of the full extent of opercular evolution now disclosed in *Dendropoma*. Its operculum is shallowly concave with neither the calcified mamilla nor the high development of the chitinous disc found in most members of the genus. It recalls much more indeed the simple opercular type found in the embryos of the vermetids in general. Further, the advanced sculptural features of the shell, the corroding habit and the very characteristic nucleus, together with the late appearance—so far as is known—of the genus in time, must clearly disqualify *Dendropoma* as a whole from any primitive relation with the rest of the vermetids. This genus, on the one hand, and the mucous-feeding *Serpulorbis* on the other, represent advanced forms that have followed divergent paths.

The derived condition of *Dendropoma* throws doubt in turn on my assumption that ciliary feeding was the sole primitive habit of the Vermetidae. In particular, such a view would leave unexplained the presence of a pedal mucous gland and pedal tentacles in every vermetid studied. I suggested previously that the function of this gland in its relatively small state in *Dendropoma maximum* was merely to cleanse the surface of the foot of waste particles alighting upon it, and that in *D. lamellosa* it had begun to assume some role in the feeding process. I think it safer, however, until we have actual observations of feeding in more living vermetid material, to suppose that the most general and primitive condition included the ability to collect food by both ciliary and mucous means (see page 619). Such a condition is indeed found in *D. lamellosa*, *D. irregularis*, *Petaloconchus nigricans*, *Serpulorbis zelandicus* and *S. aotearoicus*. The exclusive or predominant use of ciliary feeding would then be a later development of a few species like *Dendropoma maximum*, while among the most advanced species of *Serpulorbis* the gill has become very small and the animal develops by contrast a total reliance on mucous trap feeding.

The primitive features of *Dendropoma* are indeed much more apparent in the status of the animal than of the shell. They include the retention of the operculum the relatively small size of the mucous gland and pedal tantacles, the lack of reduction of the gill, and the lack of a pallial fissure or of shell attachment of the eggs in the female. All these features are, however, equally characteristic of *Petaloconchus*, a genus of which I have had little chance till recently for full examination of animals. *Petaloconchus*, moreover, lacks the advanced character of the operculum and the apex. Here the operculum is thin and fragile, only slightly, if at all, overlapping the foot, capable of withdrawal into the shell and distinguishable from the larval operculum only in the raised spiral flange of its free surface. The apex is multispiral, with three to four whorls. In *P. montereyensis* and in *P. nigricans* the pedal mucous gland and pedal tentacles are of moderate size and the gill shows primitively triangular filaments with little sign of reduction. There is no channelled food groove as in some *Dendropoma*, and it is a fair inference from anatomy that most *Petaloconchus* possess both modes of food collecting, neither excessively developed.

Petaloconchus has several features removing it from fully primitive rank, in particular the characteristic shell coiling which there is no reason to suppose was an early feature in the family and the possession of a long tailpiece secreting longitudinal internal lamellae. In addition, there is no record of its early representation among fossil vermetids. The specialised features of the internal lamellae are avoided by forms like *Vermetus* (*Thylaeodus*) *contortus*, (otherwise a good *Petaloconchus*), *Vermetus adansonii* and *V. triqueter*, with long pedal tentacles and large mucous gland, and (at least in *V. triqueter*), with mantle slit, and shell attachment of eggs, seem thoroughly committed in the *Serpulorbis* direction of evolution.

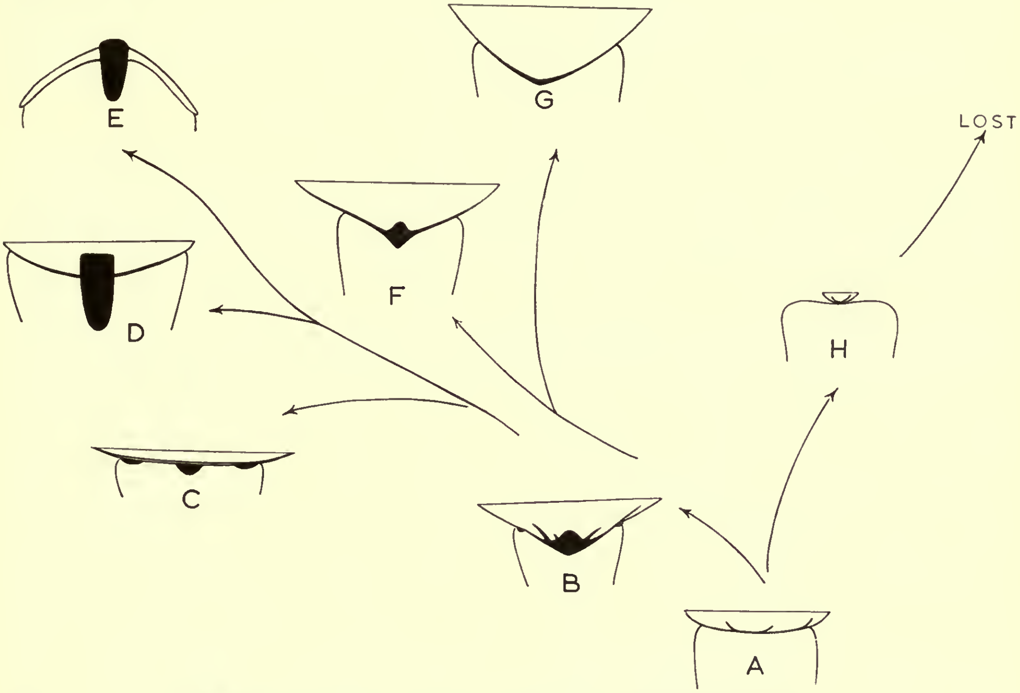


FIG. 15. A suggested sequence in the evolution of the operculum of the Vermetidae. A generalized basic form (lower right) represented by *Petaloconchus* species, is shown giving rise to the reduced condition in *Vermetus* and to the variant conditions found in *Dendropoma*. A. *Petaloconchus*. B. *Dendropoma marchadi*. C. *D. rastrum*. D. *D. lamellosa*. E. *D. thalia*. F. *D. megamastum*. G. *D. maximum*. H. *Vermetus*.

A more reliable approach to phylogeny, based on non-adaptive features, may stem from the evidence of the operculum and the apex ; these features harmonise very well (see Text-figs. 14, 15), and they moreover agree with the tentative dichotomy—based on a study of the animal—suggested by me in 1955. On this basis, the multispiral apex of *Petaloconchus* would denote a central and primitive position, giving rise to the somewhat shorter-spired apex of most *Serpulorbis* and of *Vermetus* s.s. and to the large and paucispiral apex of *Dendropoma*. With differences in apex are to be expected differences in the life history and habits of the veliger. The genus *Dendropoma* is likely to have lost the free-swimming habits, but a free-swimming stage persists in at least one *Serpulorbis* species (*S. imbricata*) and should be looked for in species of *Petaloconchus.*[1] Similarly with the opercula, *Petaloconchus* differs only from the larva in the spiral lamella acquired by its thin fragile operculum; *Vermetus* s.s. has a similar operculum reduced to a vestigial button; *Serpulorbis* has lost the operculum altogether and *Dendropoma* has become greatly specialized in the operculum, which develops a calcified axial mamilla and may consist of a concave bowl, a flat disc or a strong elevated dome. *Dendropoma marchadi* combines the characters of *Dendropoma* and *Petaloconchus,* with a concave bowl provided with both a mamilla and a spiral flange. As well as in the reduction of the operculum, *Vermetus* s.s. runs close to *Serpulorbis* in the high development of the pedal gland and pedal tentacles and in the pallial fissure and mode of attachment of the eggs. The radula abundantly confirms the relationship of *Serpulorbis* with *Vermetus* s.s. and also the approximation of *Petaloconchus* towards *Dendropoma.*

Evolution of vermetids is a mosaic affair; and a common ancestor with the whole complex of assumed primitive characters we shall not expect to find; the phyletic morphologist must be content if he can discern something of the direction and extent of the various evolutionary trends. This much can be tentatively claimed; that the earliest vermetids must have possessed many of the features of the operculum and apex of *Petaloconchus*; they must have already possessed pedal gland and pedal tentacles, employed for putting out feeding mucous traps to assist the ciliary action of the gill; the gill retained its normal mesogastropod form, with the filaments unspecialized and triangular; the foot carried a full-sized operculum, thin and flatly concave, possibly with a spiral flange; the mantle of the female was entire, with the eggs lying unattached in the mantle cavity; the shell had equally developed longitudinal and spiral sculpture, and showed neither corroding habit nor internal septa; and the larva very probably showed a period of free-swimming.

Serpulorbis, according to Keen, appears earliest in time, in the Eocene. Species with the *Petaloconchus* mode of coiling are found first in the Early Miocene, *Dendropoma* doubtfully in the Oligocene. Palaeontological evidence would generally be allowed great weight in determining the early or primitive section of the Vermetidae. Yet in view of the lack of the apex or operculum in fossils, such evidence cannot be conclusive; and the problem must be attacked independently by comparative morphology in its own right. In the sculpture and mode of coiling of the shell (as well as in the multispiral apex) *Serpulorbis* is suitably unspecialized for an early vermetid. Yet, as pointed out earlier, the animal discloses many advanced features. The operculum is lost, the pedal tentacles and mucous gland are highly emphasized, the mantle is slit in the female and the eggs are attached to the interior of the shell. The condition of *S. gigas,* with the gill reduced and functionless in feeding, may be held to represent the ultimate advance characteristic of this evolutionary line.

4. ABSTRACT

The adaptive morphology of the Vermetidae is considered in the light of our knowledge of the habits and functions of the living animal, especially in relation to the mechanisms of mucous and ciliary feeding and the mode of brood protection.

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[1] See Robertson's observation on *P. nigricans* (page 615).

In a larger range of species a comparative study has been made of the anatomical features of the animal, including the operculum, the organs of the pallial cavity, the radula and the rest of the digestive system, and the reproductive system. The bearing of this evidence upon evolution and phylogeny has been supported with a consideration of the embryonic shell.

The nature and direction of the evolutionary trends operating within this family has been discussed and a broad picture of the suggested generic relationships and divergence is presented. The family, as properly restricted, has been found to consist of a few well-marked genera ; and the naturalness of the four main genera, *Vermetus*, *Dendropoma*, *Petaloconchus* and *Serpulorbis*, in the sense proposed by Dr. Myra Keen, has been amply confirmed from the malacological standpoint.

5. ACKNOWLEDGMENTS

During the whole course of my study of the Vermetidae, I have had access to the kindness and sound counsel of Dr. Myra Keen and have had the pleasure of collaborating with her both in correspondence and during her visit to London. My views upon the evolution of the Vermetidae owe very much to Dr. Keen's profound insight into the conchology and history of the family.

I wish also to acknowledge the courtesy and help of the Trustees and officers of the British Museum (Natural History) in making available for my study the whole range of the vermetid material represented in their spirit collections.

REFERENCES TO FIGURE CAPTIONS

ALB	albumen gland
AN	anus
BCV	body cavity
BUC	buccal cavity
CAPS A	aperture of capsule gland
COL	columellar muscle
CPS	capsule gland
CT	ctenidium
C TE	cephalic tentacle
DIG	digestive gland
DIG A	anterior lobe of digestive gland
DIG P	posterior lobe of digestive gland
E	eye
E CP	egg capsules
EMB	embryos
F	foot
FAE	faecal pellets
F GR	food groove
FL	gill filament
F TR	food tract
GON	gonad
HYP	hypobranchial gland
INT	intestine
J	jaw
K	kidney
LAM	spiral lamella of operculum
M	mouth
MA CAV	mantle cavity
MUC	mucus from pedal gland
OD	odontophore
OES	oesophagus
OP	operculum
OP M	opercular mamilla
OS	osphradium
OVD	oviduct
PA	mantle
PA C	cut edge of mantle
PA SL	pallial slit of female
PD D	duct of pedal mucous gland
PD G	pedal mucous gland
PD T	pedal tentacle
PR	proboscis
RA	radula
RA S	radular sac
REC	receptaculum seminis
RM	rectum
S	reduced sole of foot
SAL	salivary gland
SH	shell
ST	stomach
ST C	style sac
VISC	visceral mass

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